

# Ptyctodontid fishes (Vertebrata, Placodermi) from the Late Devonian Gogo Formation, Western Australia, with a revision of the European genus *Ctenurella* Ørvig, 1960

John A. LONG

Department of Earth and Planetary Sciences, The Western Australian Museum, Francis Street, Perth, Western Australia, 6000 (Australia)

Long J. A. 1997. — Ptyctodontid fishes (Vertebrata, Placodermi) from the Late Devonian Gogo Formation, Western Australia, with a revision of the European genus *Ctenurella* Ørvig, 1960. *Geodiversitas* 19 (3) : 515-555.

## ABSTRACT

A new, almost complete specimen of the ptyctodontid placoderm *Campbellodus decipiens* Miles et Young, 1977 enables description of the skull roof, trunk shield, visceral skeleton, pelvic girdle, dermal scale cover, and parts of the vertebral column. A new reconstruction of the head shield of *Ctenurella gladbachensis* Ørvig, 1960 from Bergisch-Gladbach permits this taxon to be generically defined from the Gogo species previously referred to that genus. The Gogo form is here referred to *Austroptyctodus* n.g. A new specimen of *Austroptyctodus gardineri* Miles et Young, 1977, together with new observations of *Chelyophorus verneuili* Agassiz, 1844 and *Ctenurella gladbachensis* Ørvig, 1960, shows new information for the endocranium, the hyoid arch and visceral skeleton, identifying the previously identified "metapterygoid" elements as paired nasal bones. The large visceral skeleton bone posterior to the jaw joint in ptyctodontids is here identified as an elongated interhyal.

## KEY WORDS

Ptyctodontida,  
Devonian,  
Placodermi,  
Gogo,  
Australia,  
*Austroptyctodus* n.g.,  
*Ctenurella*,  
*Chelyophorus*.

## RÉSUMÉ

Une nouvelle description du toit crânien, de la cuirasse thoracique, du squelette viscéral, de la ceinture pelvienne, de l'écaillure et de quelques éléments de la colonne vertébrale est proposée à partir d'un nouveau spécimen sub-complet du ptyctodonte *Campbellodus decipiens* Miles et Young, 1977. Une nouvelle reconstitution du toit crânien de *Ctenurella gladbachensis* Ørvig, 1960 (Frasnien de Bergisch-Gladbach, Allemagne) permet de redéfinir le genre *Ctenurella*, en y incluant les formes de Gogo qui y sont rapportées. Un nouveau genre *Austroptyctodus* est créé. À partir du matériel qui définit *Austroptyctodus gardineri*, espèce-type du genre, et d'une révision de *Chelyophorus verneuilli* Agassiz, 1844 et de *Ctenurella gladbachensis*, de nouvelles informations sur l'endocrâne, l'arc hyoïde et le squelette viscéral des ptyctodontes sont fournies. Ainsi le « métapterygoïde » est interprété comme des os nasaux paires, de même l'os du squelette viscéral situé en arrière de l'articulation de la mandibule serait un interhyal de forme allongée.

## MOTS CLÉS

Ptyctodontida,  
Devonien,  
Placodermi,  
Gogo,  
Australie,  
*Austroptyctodus* n.g.,  
*Ctenurella*,  
*Chelyophorus*.

## INTRODUCTION

The ptyctodontid placoderms have for many years been a problematic and poorly-known group of extinct fishes. Early workers identified ptyctodontids only from their characteristic tooth plates and thus allied them to the holocephalans (Pander 1858; Woodward 1891), although when the exoskeletal trunk armour was described by Jaekel (1907) he compared it favourably with the sturgeon *Acipenser*, an osteichthyan fish. Both Dollo (1907) and Goodrich (1909) rejected this view and argued that they were placoderm fishes. Watson (1934) described more complete material of a new form he called *Rhamphodopsis* and further characterised them as placoderm fishes, and this view was strengthened by further discoveries of well-preserved specimens (Watson 1938). Major discoveries of complete, well-preserved ptyctodontids from the Bergisch-Gladbach region of Germany described by Ørvig (1960, 1962, 1971, 1980) led him to revive the earlier hypothesis of a holocephalan affinity between ptyctodontids and holocephalans, proposing them to be ancestral to the holocephalans, an opinion followed by Stensiö (1963, 1969) and Jarvik (1980). However, many researchers working with placoderm fishes or chondrichthyans opposed this view, regarding ptyctodontids as placoderm fishes (e.g. Patterson 1965; Stahl 1967; Miles 1967; Miles & Young 1977; Denison 1978; Forey & Gardiner 1986; Young 1986). Today this view is widely held, and the placoderm affinity of ptyctodontids has been borne out by several recent computer analyses of placoderm interrelationships (e.g. Forey & Gardiner 1986; Carr 1991, 1995; Goujet & Young 1995).

The problematic position of the group within the Placodermi has been raised. They have been proposed as a primitive sister group to other placoderms (Miles & Young 1977; Young 1980), as a primitive group more derived than acanthothoracids plus rhenanids, but plesiomorphic to all other placoderms (Forey & Gardiner 1986), or as a sister taxon to the petalichthyids (Goujet 1984; Goujet & Young 1995; Carr 1995).

Most of the known ptyctodontid taxa (some forty-seven species, Carr 1995, amended) are based solely on tooth-plates (Denison 1978),

although the following species have been described from relatively complete, well-preserved material of head and trunk armour: *Ctenurella gladbachensis* (Ørvig 1960, 1971), *Austroptyctodus gardineri* n.g. (Miles & Young 1977, here erected as a new genus), *Rhamphodopsis threiplandi* and *R. trispinatus* (Watson 1934, 1938; Miles 1967), *Rhynchodus tetrodon* (Newberry 1873; Jaekel 1903; Gross 1933; Stensiö 1959; Miles 1967), *Chelyophorus vernueili* (Agassiz 1844; Eichwald 1859; Obrucheva 1983), and *Ptyctodopsis menzeli* (Denison 1985). Recent new discoveries of other relatively complete ptyctodontids have been made in North America from the Frasnian Mt. Elden site in Arizona (Johnson & Elliott, in press) and from the Pinicon Range Formation, Iowa (Hickerson 1993; work in prep.).

The superb three-dimensionally preserved material of ptyctodontids from the Frasnian Gogo Formation of Western Australia has provided the most detailed knowledge of the group to date. Miles & Young (1977) described several specimens of a new species they assigned to the genus *Ctenurella* Ørvig, 1960. Two incomplete specimens were placed in the new genus and species, *Campbellodus decipiens*. Further observations on the structure of the Gogo "*Ctenurella*" were described by Gardiner (1984a) and Forey & Gardiner (1986). New finds of Gogo fishes made during expeditions in 1986-1989 by the author include many new arthrodires (Long 1987, 1988a, 1988b, 1990b, 1994a, 1995b) as well as two nearly complete, articulated specimens of ptyctodontids, which belong to the previously described taxa.

The aim of this paper was originally to describe this new material of the Gogo ptyctodontids in detail, by comparison with other specimens of ptyctodontids, made available for the author to study at the Muséum national d'Histoire naturelle. The well-preserved nature of the Gogo specimens has permitted new further interpretations of the structure of these other taxa. Comparisons with the Bergisch-Gladbach *Ctenurella* indicated that its skull roof and visceral skeleton could be reinterpreted. It soon became apparent that this species differs in several major features from the Gogo species, and thus a new genus, *Austroptyctodus* n.g., is here erected for the Gogo species.

## DERMAL BONE TERMINOLOGY IN PTYCTODONTIDS

The central median bone that bears the X-shaped confluence of the two main dorsal sensory-line canals has been previously called the centro-nuchal (Ørvig 1960), the centro-median (Miles 1967), the nuchal (e.g. Miles & Young 1977; Long 1988a) or the postpineal (Denison 1978, 1985; Johnson & Elliott 1996). Confusion over the name of this bone has arisen, largely due to the supposed presence of a small posterior median element in *Rhamphodopsis* which was termed the nuchal. Examination of specimens of *Rhamphodopsis threiplandi* in the collections of the Natural History Museum, London, and in the Field Museum, Chicago, shows that the posterior nuchal element is not present in this genus, but was misinterpreted by Watson due to the crushed and fractured nature of the Edderton specimens. The area of exposed bone immediately behind the paired central plates is most likely the crushed occipital ossifications of the braincase, as this region lacks any trace of dermal ornamentation on the Edderton specimens.

In other placoderm groups that have the supra-orbital sensory line canals as well as posterior pit-line canals converging mesially onto one median bone, as in ptyctodontids, this bone is generally identified as the nuchal, especially so when it extends all the way to the posterior margin of the skull roof (e.g. as in petalichthyids; Woodward 1941; Gross 1963; Young 1985; Liu 1992). This condition is also seen in the primitive arthrodire-like form *Wuttagoonaspis* (Ritchie 1973) and in phyllolepid, where the nuchal plate is broad rather than elongate, but still bears the confluence of several sensory-line canals (Long 1984b). In many primitive arthrodires this bone has a similar elongate shape and also has similar contact relationships with neighbouring paranuchal, central, and postorbital or preorbital bones, although the convergence of the sensory-line canals is lacking.

Thus the median canal-bearing bone in ptyctodontids is interpreted here as homologous to the nuchal of other primitive placoderms, rather than a postpineal as this element, where present

in some placoderm groups, is always a median bone lacking sensory-line canals (e.g. as in antiarchs, Denison 1978), or maybe represented by a series of irregularly-shaped anamestic bones (as in the rhenanid *Asterosteus*, Stensiö 1969, fig 92). For the other bones in the head shield and cheek of ptyctodontids, papers published since Miles & Young (1977) use a consistent terminology. However, the large paired ventral bones in the trunk shield that have been called either the anterior ventrolaterals (Gross 1933; Miles 1967) or the interolaterals (Watson 1938; Denison 1978, 1985) require discussion. Ørvig (1960) regarded them as a combination of both elements and termed them the interolateral-anterior ventrolaterals. The anterior ventrolateral plates in primitive placoderms, such as petalichthyids (*Lunaspis*, Gross 1961), early arthrodires (actinolepids, phyltraenaspid, Goujet 1984b), phyllolepid (Long 1984b) and *Wuttagoonaspis* (Ritchie 1973) are named so because there is also a posterior ventrolateral plate present posterior to them. All of these forms also bear paired interolateral plates forming the anterior ventral margin of the shield and meeting the spinal plates dorsally, and in all cases having an expanded anteriorly-facing postbranchial lamina with rows of triangular tubercles. In acanthothoracids (e.g. *Romundina*, Ørvig 1975) and rhenanids (e.g. *Jagorina*, Stensiö 1969) there is only one pair of large ventral plates and these also form the anterior margin of the ventral lamina of the trunk shield and have a postbranchial lamina which in life presumably formed the posterior wall of the branchial chamber. However, it is known that the position of the scapulocoracoid in arthrodires generally sits between the anterior lateral, the spinal and the anterior ventrolateral plates (and also between the interolateral in *Dicksonosteus*, Goujet 1984b). Similarly, in antiarchs, it lies within the bounds of the anterior ventrolaterals, even though only remnants of it have been found in primitive forms (e.g. *Procondylolepis*, Young & Zhang 1992). Thus its condition in ptyctodontids would imply that the interolateral has expanded ventrally to include the scapulocoracoid, or that it has indeed fused with the anterior ventrolateral to be a compound bone (as suggested by Ørvig 1960, also Stensiö 1959). The identifi-

cation of the bones in ptyctodontids comes down to the overall shape in that they are narrow bones without posteriorly extended ventral laminae, bordering, in the trunk shield, the anterior ventral margin of the trunk and contacting the spinal plate dorsally, and the fact that they bear the well-developed postbranchial lamina with rows of triangular tubercles, a feature never found in any placoderm anterior ventrolateral plate (because interlaterals are also present in the same armour). Thus it is here suggested that they represent interlateral plates. This hypothesis implies that the ptyctodontid trunk shield is more specialised than those of other placoderms in the secondary loss of both anterior and posterior ventrolaterals. In this respect they could parallel the evolution of phyllolepid, now regarded as derived arthrodires in the loss of posterior dorsolateral plates and the fusion of upper jaw elements (based on materials of a new phyllolepid from New South Wales under study by Dr. A. Ritchie, pers comm. 1995).

## MATERIALS AND METHODS

The ptyctodontids from Gogo were prepared by the standard acetic acid technique using about 5-10% concentration, strengthened with dilute B30 Mowital in acetone solution (from Hoescht). The delicate nature of the *Austroptyctodus* specimen called for epoxy resin transfer preparation. Before embedding the specimen in resin, a latex peel of the exposed surface detail was made. All photographs are of specimens whitened with ammonium chloride, except for the Bergisch Gladbach specimens which were photographed under alcohol.

The new Gogo specimens were compared with the following ptyctodontid material. These results will form the basis of a future revision of the Euramerican ptyctodontids:

– *Austroptyctodus gardineri* n.g. (Miles *et* Young, 1977). All specimens held in the Natural History Museum, London. Upper Devonian (Frasnian), Gogo Formation, Western Australia.

– *Chebyphorus verneuli* Agassiz, 1844. Original Agassiz collection held in the Palaeontological collections of the Muséum national d'Histoire

naturelle, Paris. Upper Devonian (Fammenian), Dankov-Lebedyan beds, USSR.

– *Ctenurella gladbachensis* Ørvig, 1960. Five nearly complete well-preserved specimens held in the Palaeontological collections of the Muséum national d'Histoire naturelle, Paris; other specimens in the Natural History Museum, London. Middle-Upper Devonian (Upper Givetain/Lower Frasnian), Oberer Plattenkalk, Germany.

– *Ptyctodopsis menzelli* Denison, 1985. Type specimen held (on display) in the County Museum, Iowa City, Iowa; additional specimens held in the Geology Department collection, University of Iowa, Iowa City. Middle Devonian (Upper Givetian), Cedar Valley Limestone, USA.

– *Rhamphodopsis threiplandi* Watson, 1934. Specimens in the Field Museum, Chicago and in the Natural History Museum, London. Middle Devonian (Eifelian), Middle Old Red Sandstone, UK.

– *Rhynchodus tetradon*. Cast of the holotype held in the Natural History Museum, London. Upper Devonian (Frasnian), Kellwasserkalk, Germany.

– Specimens of an undescribed new genus of ptyctodontid from the Spring Grove Member (Givetian), northern Illinois, held by the Geology Department, Augustana College, Rock Island, Illinois.

– Specimens of an undescribed new genus of ptyctodontid from the Gneudna Formation (Upper Givetian-Lower Frasnian), Western Australia, collected by the author and K. Trinajstić in 1995.

All specimens described or cited in this paper are deposited in the palaeontology collections of the following institutions as denoted by these abbreviations:

|      |  |
|------|--|
| MNHN | Muséum national d'Histoire naturelle, Paris;         |
| NHM  | Natural History Museum, London;                      |
| WAM  | Western Australian Museum, Perth, Western Australia. |

## SYSTEMATIC DESCRIPTIONS

### Genus *Campbellodus* Miles *et* Young, 1977

TYPE SPECIES. — *Campbellodus decipiens* Miles *et* Young, 1977.



AMENDED DIAGNOSIS. — A moderately large ptyctodontid having a *Ptyctodus*-like crushing dentition with high dorsal process on the upper toothplate; head shield having a breadth/length ratio of 90, the nuchal is subrectangular, almost as broad as long and participates in the posterior margin of the skull-roof, excluding the centrals from mesial contact; submarginal plate is much deeper posteriorly than anteriorly. Trunk shield with three median dorsal bones, the dorsalmost being a broad, flat spine. Spinal plate very small; anterior median ventral plate more than twice as broad as long. Tail covered with large overlapping scales.

*Campbellodus decipiens* Miles et Young, 1977

*Campbellodus decipiens* Miles et Young, 1977: 145-155, figs 8-14, pls 1, 2A, B, 4A. — Denison 1978: 28. — Long 1987a: 203; 1988a: 443-4, fig. 7; 1988c: 141, 143, 144, fig. 2B; 1991: 366, 367, fig. 20H; 1995a: 108-110.

*Ptyctodus* sp. Gardiner et Miles, 1975.

"tooth-plates resembling those of *Rhynchodus*" (Brunton, Miles & Rolfe 1969)

"tooth-plates which recall those of *Ptyctodus*" (Miles 1971)

HOLOTYPE. — WAM 70.4.252. This number is not published in the Miles & Young (1977) as the specimen had then been allocated by the provisional British Museum of Natural History number P50905.

OTHER MATERIAL. — NHM P50907, comprising the left spinal plate, left upper toothplate, incomplete left interolateral plate, partial dorsal spine, a dermal scale and parts of perichondral ossifications of the endocranium (Miles & Young 1977). WAM 86.9.672, an almost complete individual, shows the head shield mostly complete, missing only part of the posterior margin on the right side and a small part of the left posterior margin. It shows well the three-dimensional form of the entire articulated trunk shield, the pelvic girdle and endogirdle, body scales and axial skeletal elements. WAM 95.6.112 shows the left upper and lower tooth plates, mirror opposites to those seen in the holotype.

REMARKS. — The new material is regarded as cogenetic with the holotype as the dorsal spine is of the same broad based shape with similar ornamentation, and the isolated preorbital, postorbital and submarginals of the Holotype are all of similar shape and identical proportions in WAM 86.9.672. This genus has been redefined in the light of nearly complete material of the dermal armour, axial skeleton and squamation. Long (1988a) figured a reconstruction of the dermal armour, and commented briefly on its overall morphology, but it is only within the framework of stu-

dying the other Gogo ptyctodontid with the comparative material of other European genera that the complete description, and new reconstruction provided here, could be undertaken.

DESCRIPTION

*Head shield*

The exceptional preservation of WAM 86.9.672 (Figs 1A-C, 2) has enabled the head shield of *Campbellodus* to be restored in its natural three-dimensional form. This is unique for ptyctodontids in which restorations usually show the head shield flattened in dorsal aspect, the one exception being *Ptyctodopsis* (Denison 1985) which is preserved in lateral view. Overall the head shield is 90% as broad as long, being broadest across the postorbital plates posterior to the large orbit. The preorbital plates are exceptionally large, about twice the size of the other skull roof bones, which are approximately the same size as each other. An unusual feature of the skull roof is that the preorbital plates are not in mesial contact with apparently an open pineal notch for the pineal organ. No pineal plate was recovered during the preparation of the specimen, and, as most of the delicate gill arch elements of both sides were found, it is assumed that a pineal plate was either very small (as in *Austroptyctodus* n.g.), or absent. In lateral view, the skull roof shows a slit-like opening at the junction of the postorbital, marginal and submarginal plates, referred to previously by Miles & Young (1977) as the postorbital fenestra and by Long (1988a) as the spiracular slit.

**Marginal plate.** It was apparently not tightly connected with the lateral margin of the head shield; as its precise dorsal border does not correspond to the well-preserved ventral margin on the lateral face of the head shield, it is presumed to have been loosely attached. The submarginal was probably also free in the skin of the cheek region, but anteriorly contained the opercular cartilage which articulated with the ethmoid ossification of the braincase.

**Preorbital plates.** (PrO; Figs 1A-C, 2) These are the largest bones of the head, being just over half the total length of the skull. Miles & Young (1977, fig. 8) described and figured one of these plates but wrongly identified it as the right ele-



FIG. 1. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. **A-C**, head shield; **A**, dorsal view; **B**, ventral view; **C**, right lateral view. **D, E**, right marginal plate; **D**, lateral view; **E**, mesial view. **F-H**, median dorsal plates in right lateral view; **F**, median dorsal spine; **G**, median dorsal plate 2; **H**, median dorsal plate 1. **I, J**, prepelvic bone and attached endoskeletal pelvic girdle; **I**, ventral view; **J**, dorsal view. **K**, right quadrate in mesial view. All photos whitened with ammonium chloride.

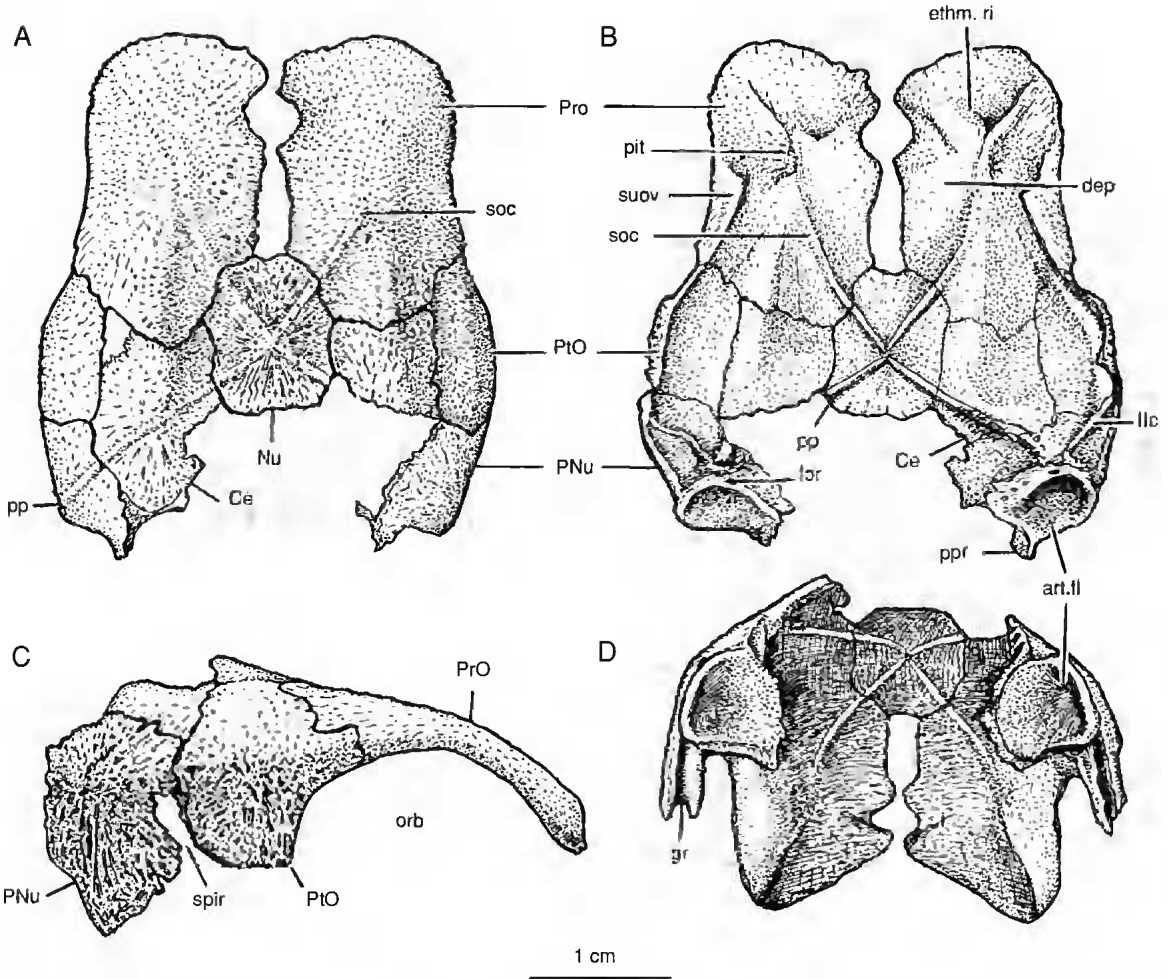


Fig. 2. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. A-D, sketch of head shield; A, dorsal view; B, ventral view; C, right lateral view; D, posterior view. **art.fl**, articular flange of neck joint on PNu plate; **Ce**, central plate; **dep**, depression; **ethm.ri**, ethmoid ridge; **for**, foramen; **gr**, groove; **llc**, main lateral line canal; **Nu**, nuchal plate (posterior element); **orb**, orbit or orbital margin; **P**, pineal plate or space provided for it in the head shield; **pit**, pit for insertion of eye muscles; **PNu**, paranuchal plate; **pp**, posterior sensory-line canal on head shield; **ppr**, posterior process of PNu plate; **PrO**, preorbital plate; **PtO**, postorbital plate; **soc**, supraorbital sensory-line canal; **spir**, spiracular slit; **suov**, supraorbital vault.

ment when in fact it is the left preorbital plate, as verified by direct comparison with the articulated head shield of WAM 86.9.672. The preorbital plates are subrectangular in form, having a breadth/length index of between 56-60, for both specimens. They show a weakly concave lateral margin, gently convex anterior margin, strongly convex posterior margin, and gently concave mesial margins with a well-defined anterior notch for the pineal foramen. In lateral view (Figs 1C, 2C), the preorbital plates are weakly

curved, flexing over the mid-point of the orbit. The path of the supraorbital sensory-line canal is only visible in dorsal view in the posterior part of the plate, faintly seen mainly through a single row of minute pores opening from within the spaces of the reticulate ornamentation. In visceral view, the tubular sensory-line canals are clearly seen (Fig. 2B, soc, pp, llc), disappearing within the centre of the bone at the ossification centre of the plate. The main lateral line sensory-line canal that comes off the marginal plate enters the

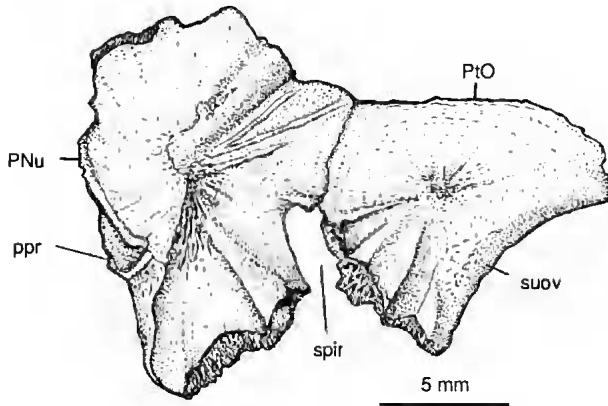


FIG. 3. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. Left paranuchal and postorbital plates in mesial view, showing spiracular slit. PNu, paranuchal plate; ppr, posterior process of PNu plate; PtO, postorbital plate; spir, spiracular slit; suov, supraorbital vault.

preorbital at its posteroventral corner and runs directly into the ossification centre of the plate. In visceral view, the preorbital shows areas of cancellous spongy bone above the orbits, forming a supraorbital vault (suov, Fig. 2B), and smooth areas of bone surface for contacting the endocranium, presumed here to be mostly cartilaginous. An anteriorly facing depression (Fig. 2B, ethm.ri) is posteriorly bounded by the raised supraorbital sensory-line canal (soc) and a mesially directed ridge. Presumably, this region braced the dorsal wall of the ethmoid division of the braincase as it does in arthrodires. The lateral sides of the supraorbital sensory-line canal has a pit (Fig. 2B, pit) just posterior to the ethmoidal ridge, possibly a myodome for eyemuscle attachment. There is a broad triangular depression (Fig. 2B, dep) defined by the mesial margin of the supraorbital canal and the raised mesial edge of the supraorbital vault, and a similar posteriorly facing depression between the two converging sensory-line canals in the posterior half of the plate. The ornament of the preorbital plate is largely reticulate with patches of very fine tubercles over the orbits and towards the anterior margin.

**Postorbital plate.** (PtO; Figs 1A-C, 2, 3) It is only partially visible in dorsal view, showing its largest area in lateral view. Its dorsal lamina contacts the central posteriorly and is notched into the preorbital anteriorly. In lateral view, it has a smoothly concave anterior margin for the orbit and an irregularly convex posterior margin which in part forms the margin for the spiracular slit (spir; Figs 2C, 3). In visceral view, it shows

no unusual features apart from linear thickenings of bone running out from the ossification centre to the margin of the spiracular slit (Fig. 3). These thickening of bone around the spiracular slit presumably assisted to direct the flow of water from outside into the spiracular groove.

**Nuchal plate.** (Nu; Figs 1A, B, 2A, B, D) This central median bone of the skull roof is contacted anterolaterally by the preorbitals, laterally by the centrals, and forms the posterior indented margin of the skull roof. It is a relatively small but broad bone for pycnodontids, about half as long as the preorbital, and only a little longer than its breadth. It is quite flat. Its margins are all complete and gently concave to meet the surrounding bones which it overlaps. The confluence of the sensory-line canals on the nuchal are well-defined in dorsal view and, in ventral view, are clearly seen by the raised tubes of bone that carried the sensory-lines (pp; Fig. 2B). Weak ridges of bone radiate outwards from its ossification centre.

**Left central plate.** (Ce; Figs 1A-C, 2A) It is well-preserved in this specimen although only part of the right element is present, but neither shows the posteromesial margin completely preserved. It has a strongly concave anterior margin for the preorbital plate, straight contact of lateral margin where it meets the marginals, a strongly convex lateral contact margin with the paranuchal plate, and a relatively straight mesial margin where it lies in contact with the nuchal. The short region of the posteromesial margin is also quite straight and forms part of the indented posterior margin of the skull roof.

**Paranuchal plate.** (PNu; Figs 1A-C, 2A-D, 3) It is well preserved on the left side of the skull roof; and partly preserved on the right side. It has an irregular shape, dominated by concave margins where it contacts the postorbital anteriorly and the central anteromesially. It has short contact with the postorbital before being indented for the spiracul slit (spir; Fig. 3). The posterior margin of the paranuchal has a large, unornamented posteriorly-facing flange of bone (art.fl; Fig. 2D) for contact with the similarly flat process on the anterior dorsolateral plate (art.con, Figs 13, 14). The ventral margin of this articular flange has a small foramen (for; Fig 2B), corresponding well to the position of the endolymphatic duct opening on the visceral surface of the plate in arthrodires. Yet as the plate lacks an external (dorsal opening), I conclude it is possibly just a nutritive canal. As the two articular surfaces of the paranuchal and the anterior dorsolateral plates do not precisely fit together, a thin pad of cartilage probably divided the two flat processes to allow some slight degree of vertical flexibility in the neck joint. There is also a smooth process of dermal bone (ppr; Fig. 2B)

which projects posteriorly from the lateral margin of the paranuchal, and weakly overlaps the anterior margin of the articular process of the anterior dorsolateral plate. There is a groove along the posteroventral margin of the paranuchal plate in posterior view (Fig. 2D, gr; Fig. 6).

**Marginal plate.** (M; Figs 1D, E, 4, 6) It is well-preserved on the right side only. It is a wedge-shaped bone, slightly longer than the preorbitals and, with a breadth/length index of about 37, is narrower than for most other ptyctodontids. It lacks the strong inflection seen in some other forms, such as *Rhynchodus* and *Rhamphodopsis*, and is proportionately much smaller relative to the head shield than for those genera. It has an almost straight dorsal margin bordering the orbit, and relatively straight, short margins for contacting the postorbital and paranuchal plates. The visceral surface shows a pair of mesially directed laminae extending out from the centre of the plate (Fig. 4A, C, D). These laminae are triangular in dorsal view and have a roughened surface between them presumably for contact with the orbital ossification of the braincase. This structure in ptyctodontids is better preserved

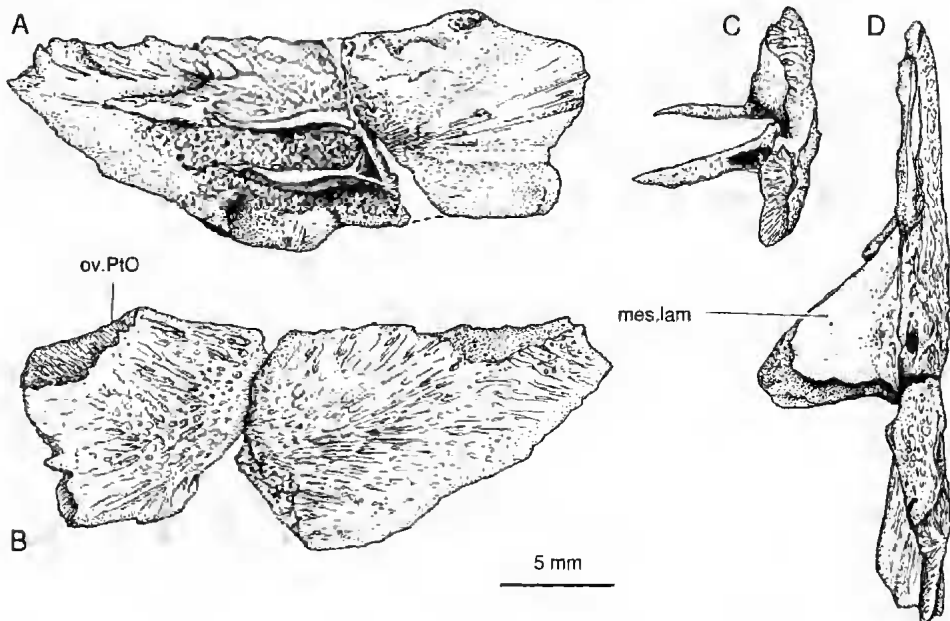


FIG. 4. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. A-D, right marginal plate; A, mesial view; B, lateral view; C, anterior view; D, dorsal view. mes.lam, mesial perichondral lamina extending from marginal plate; ov.PIO, overlap surfaces for postorbital plate.

ved in the new Gogo specimen of *Austroptyctodus* and is described in further detail below (see Figs 28, 29). The posterior division of the visceral surface of the marginal plate has a smooth triangular region emanating from behind the paired laminae. The overlap area for the postorbital plate is well-developed on the lateral surface (Fig. 4 B).

**Submarginal plate.** (SM; Figs 5, 6) It is preserved only for the left side, but is also well-preserved in the holotype and was figured and described by Miles & Young (1977, fig. 10). It is broad, posteriorly, narrowing to a slightly up-turned, well-rounded anterior end. It is proportionately deeper in its posterior end than in all other ptyctodontids for which it is known, as in most other ptyctodontid genera it is almost bar-like. The visceral surface is smooth with the anterior end having the perichondral shell of the opercular cartilage *in situ*. In ventral view, this perichondral lamina is mesially developed into a strong process (*mes.pr*; Fig. 5C), which is interpreted to have supported a thick and presumably large opercular cartilage (Fig. 6).

#### Visceral skeleton

Several paired and one unpaired perichondral ossification of the visceral skeleton were recovered from the specimen. Numerous visceral arch bones should be found in the skeleton of any fish that had them well-ossified, yet only a few bones have been found in this specimen, and in other articulated specimens of the Gogo form *Austroptyctodus*, and the German *Ctenurella*. This suggests that only some bones of the anterior gill arches in ptyctodontids were ossified. Schultze (1993: 213) points out that in elasmobranchs the dorsal hyoid arch elements are the first to chondrify (epihyal, ceratohyal), followed by the pharyngobranchials, epibranchials and ceratobranchials, then lastly by the hypobranchials and basibranchials. It is possible that only those elements of the first gill arch and possibly one posterior to it were invested with perichondral bone in ptyctodontids. This could be explained by the need to strengthen the bones in direct contact with the strong jaw mechanism, the more distal arch elements remaining as cartilaginous units.

The provisional identification of these gill arch elements is based on comparisons with articulated material of the other Gogo ptyctodontid, *Austroptyctodus*, as well as articulated specimens of *Ctenurella gladbachensis* in the MNHN, Paris. There is no direct evidence, because none of the smaller elements are preserved in life position in any specimen examined. The position and identification of the larger elements is based only on their general shape and articulation surfaces in relation to other large bones (*e.g.* the articular), and comparisons with the general shapes of these elements in other primitive gnathostomes (chondrichthyans, other placoderms, primitive osteichthyans).

The largest of the gill arch elements in *Campbellodus* are a pair of inwardly curved, distally broad elements. No comparable shape to bones previously identified in the ptyctodontid visceral skeleton by Watson (1934), Ørvig (1960), Gardiner (1984a) or Forey & Gardiner (1986). These bones (Fig. 7) are strongly curved mesially and have grooves for vascular or nerve passages on the lateral surface near the distal (smaller) end. They are too curved mesially and too narrow dorsally to be meckelian cartilages

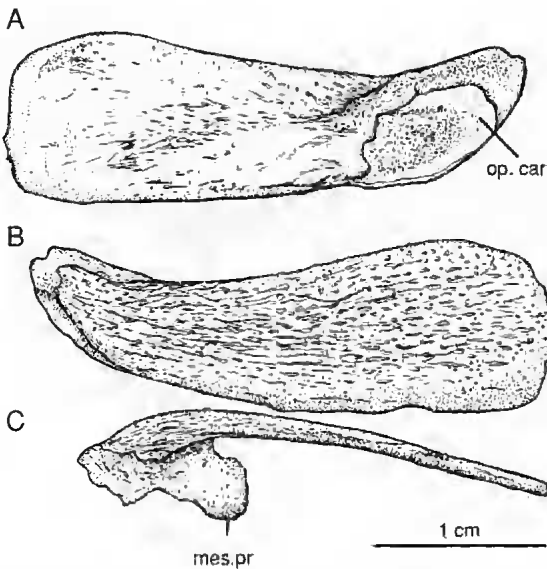


FIG. 5. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. A-C, left submarginal plate; A, mesial view; B, left lateral view; C, ventral view, showing opercular cartilage ossification. *mes.pr*, mesial process on opercular cartilage; *op.car*, opercular cartilage.



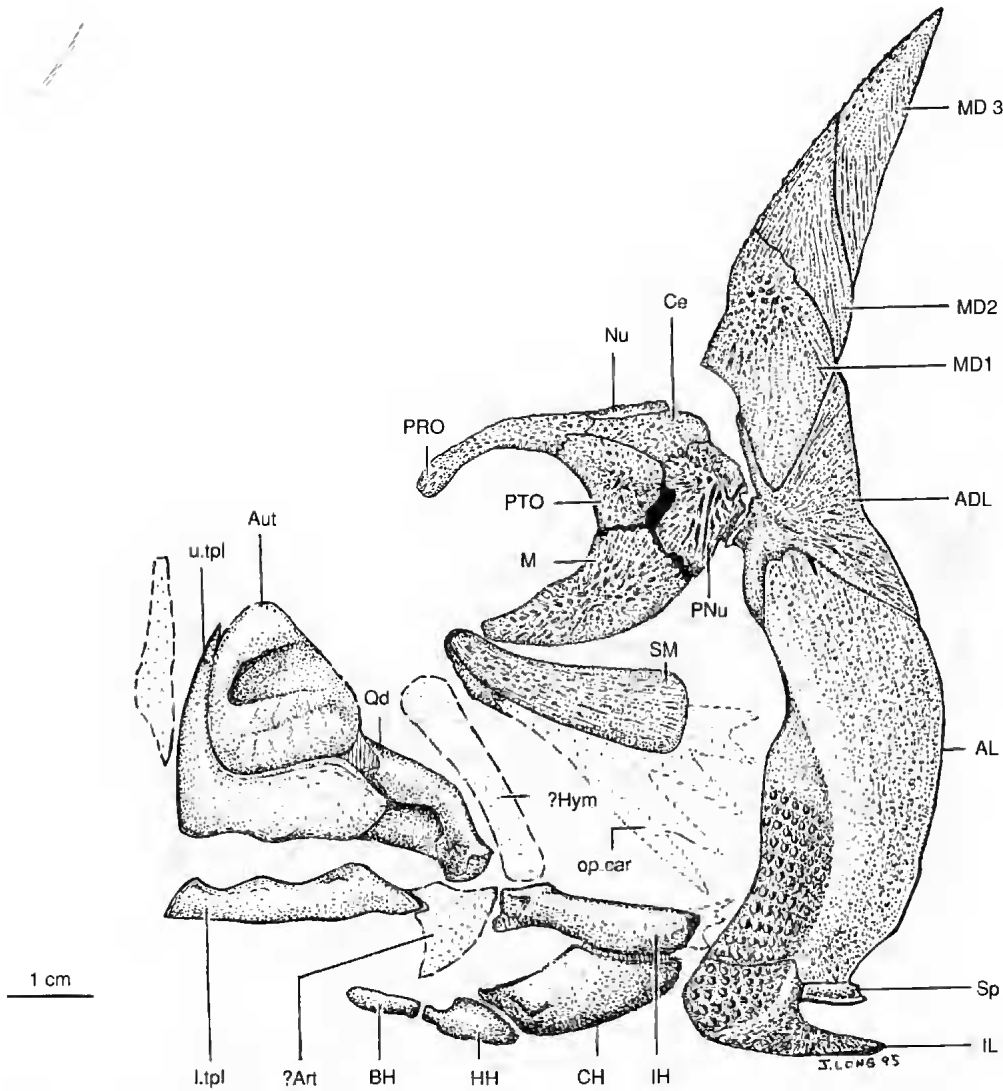


FIG. 6. — *Campbellodus decipiens* Miles et Young, 1977. Attempted reconstruction of dermal exoskeleton and visceral arches, from WAM 86.9.672. Stippled areas are hypothetically restored cartilage bones. **ADL**, anterior dorsolateral plate; **AL**, anterior lateral plate; **Art**, articular; **Aut**, Autopalatine; **BH**, basihyal; **Ce**, central plate; **CH**, ceratohyal; **HH**, hypohyal; **Hym**, hyomandibular; **IH**, interhyal element; **IL**, interlateral plate; **l.tpl**, lower tooth plate; **M**, marginal plate; **MD**, MD1, 2, 3, median dorsal plate(s) or spines; **Nu**, nuchal plate (posterior element); **op.car**, opercular cartilage; **PNu**, paranuchal plate; **PRO**, preorbital plate; **PtO**, postorbital plate; **Qd**, quadrate; **SM**, submarginal plate; **Sp**, spinal plate; **u.tpl**, upper tooth plate.

supporting the toothplates. By comparison with other gnathostome fishes they could be ceratohyals, which are also large, flat bones with mesial curvature in primitive osteichthyans like *Medoavia* (Lebedev 1995), *Glyptolepis* (Jarvik 1972) or primitive lungfishes (Miles 1977; Campbell & Barwick 1988). However it is noted that the presence of an expanded ceratohyal is

regarded as a synapomorphy of higher osteichthyans (Gardiner 1984b) as the condition in acanthodians (Miles 1973) or primitive actinopterygians (Gogo palaeoniscoids, Gardiner 1984b) is to have a slender rod-like ceratohyal of similar form to the ceratobranchials.

What therefore is the evidence for calling the elongate bone, bracing the articular in *Ctenurella*

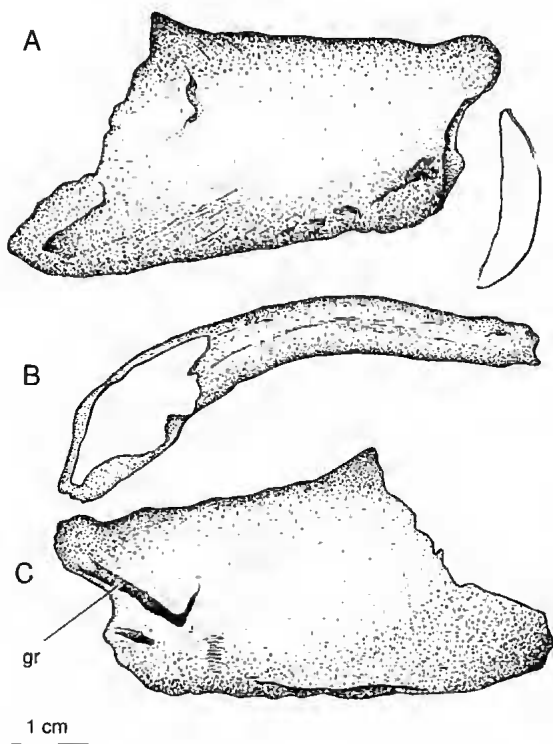


FIG. 7. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. A-C, left ceratohyal: A, mesial view; B, dorsal view; C, left lateral view. gr, groove.

*gladbachensis*, a “ceratohyal” (e.g. Forey & Gardiner 1986)? The bone lies ventral to the inferred position of the dorsal hyoidean bone, which would primitively lie next to the quadrate, and is a large bone with a complex proximal head. As restored by Forey & Gardiner (1986), it would distally meet with the restored hyomandibular and form part of a normal hyoidean arch system, except for the fact that it braces the jaw joint rather than carries on ventrally to the basi-hyal or hypohyal bones. In this respect it would be unique amongst vertebrates if regarded as a ceratohyal. I propose an alternative explanation: the elongated bone with an expanded double articular head, which braces the lower jaw, is a specialised interhyal (or “symplectic” in the terminology of Veran 1988, but not homologous with the symplectic of higher actinopterygians). Thus I regard the broad, expanded bones in *Campbellodus* as true ceratohyals that have inde-

pendently acquired the derived condition of being expanded for larger attachment area of the depressor mandibulae and interhyoideus muscle groups. Such an adaptation would benefit a specialised feeding mechanism as it occurs in ptyctodontids which were strong biters (in the ecomorphological context of Liem 1993) and thus required extreme modifications of the jaw musculature system to increase biting pressure, relative to the conservative muscle systems hypothetically restored in other placoderms such as arthrodires (e.g. Stensiö 1963; Long 1995a).

The visceral skeleton is virtually unknown in all other placoderms, apart from a serial grinding series by Stensiö (1963, fig. 8) showing only the ventral gill arch system in the arthrodire *Tapinosteus*. Thus the presence or absence of an interhyal in other placoderm groups is unknown. The function of this unusual arrangement for the expanded interhyal in ptyctodontids can only be suggested as an attachment brace for supporting the large opercular covering over the branchial lamina, possibly by attachment of additional cartilaginous opercular elements (as in the opercular cartilages of chimaerids which emanated from both the epihyal and ceratohyal elements; e.g. *Rhinochimaera* and *Callorhynchus*, Jarvik 1980, vol. 1, figs 299, 303).

The next largest bones in the visceral skeleton of *Campbellodus* are elongated paired bones with an expanded head (Fig. 8), directly comparable with the elements identified as ceratohyals by Forey & Gardiner (1986), and found in the new Gogo specimen described below, and also in articulated position in *Ctenurella gladbachensis* (see below, Fig. 25). These are not interpreted as epihyals (= hyomandibular) because of the presence of a separate epihyal in position on the new specimen of *Austroptyctodus* (Fig. 29, Hym). I regard these as interhyal elements which braced the lower jaw joint (Fig. 6, H1), the ventral most articular head meeting the small articulation surface described on the articular bone in *Austroptyctodus* (Miles & Young 1977, “arthy”, fig. 24). There is a well defined foramen at this articular head (for; Fig. 8) which may have transmitted the hyomandibular nerve. The narrow distal end of the bone is compressed laterally and ends in a slit-like articulation surface (shown in Fig. 8E), presumably for

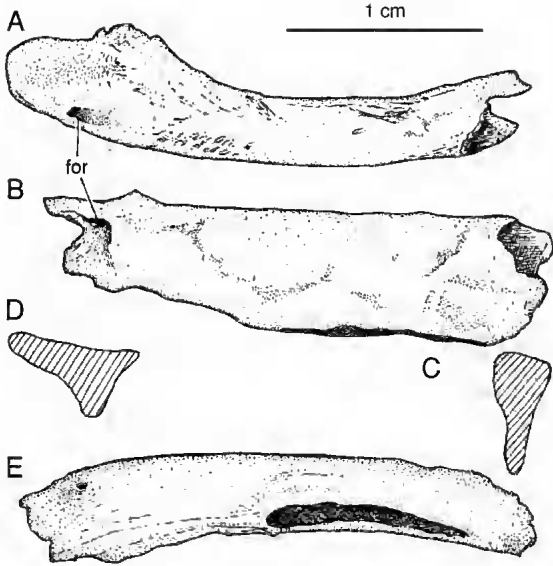


FIG. 8. — *Campbellodius decipiens* Miles et Young, 1977, WAM 86.9.672. A-D, left interhyal; A, dorsal view; B, left lateral view; C, D, cross-sections of the interhyal, respectively in distal and proximal sections; E, ventral view. for, foramen.

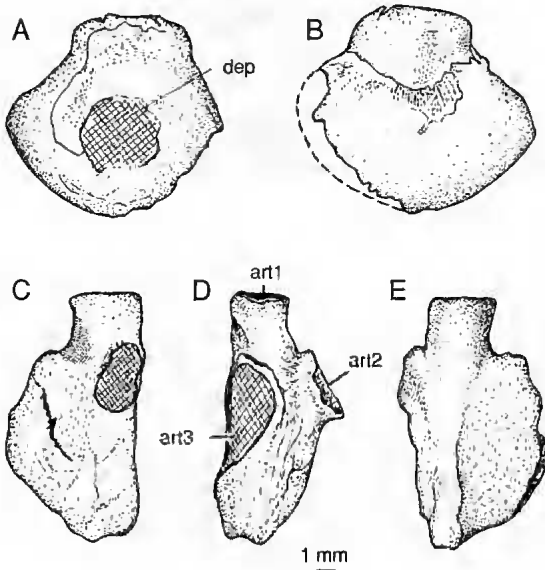


FIG. 9. — *Campbellodius decipiens* Miles et Young, 1977, WAM 86.9.672. A, B, basihyal; A, ventral view; B, dorsal view. C-E, hypohyal; C, mesial view; D, dorsal view; E, lateral view. art, articulation facets; dep, depression.

contacting the similar-sized articulation area on the ceratohyal. Two small paired elements having three articulation surfaces are here identified as possible hypohyals (Fig. 9C-E). They are flask-shaped elements with a small anterior (?) articulation surface (art 1), and two much presumed larger, mesial (art 2) and dorsal (art 3) articulation facets. The presumed dorsally-facing articulation surface is the largest of the three and matches closely with the long ventral articulation facet on the distal end of the ceratohyal. The second largest articulation is here assumed to be for mesial contact with the opposing hypohyal, as in many modern selachians (e.g. *Chlanydo-selachus*, Smith 1937). They compare well to the basic pattern of hypohyals seen in early osteichthyans (Gardiner 1984b; Lebedev 1995).

A small unpaired bone, presumably the median hyoid arch element or basihyal (Fig. 9A, B), is an almost circular bone with a single protruding articulation facet, giving it the overall shape of a circular water-canteen. This bone was identified by Gardiner (1984a, fig. 3) and by Forey & Gardiner (1986) in *Austroptyctodus* as the urohyal, yet this identification was based only on its overall shape as it was found only in one specimen, and in which case the gill arch bones were not in natural articulation. The author's identification of the element as a basibranchial is based on the fact that only one large median element of the ossified hyoid arch is present in *Campbellodius*, and that bone is therefore most likely to be the basihyal. Its rounded overall morphology is similar to that of the osteolepiform *Medoevia* (Lebedev 1995). The single articulatory facet faced posteriorly and accommodated the smaller anteriorly facing articulatory surfaces on the hypobranchials, or alternatively, may have met with a second smaller medial basibranchial element.

#### Dentition and jaw cartilages

The toothplates and jaw cartilages of *Campbellodius* have been well-described and figured by Miles & Young (1977), and Long (1988b) described an isolated upper jaw toothplate of *Campbellodius* sp. from the slightly younger Napier Range, to the west of Fitzroy Crossing. New material of *Campbellodius* showing the

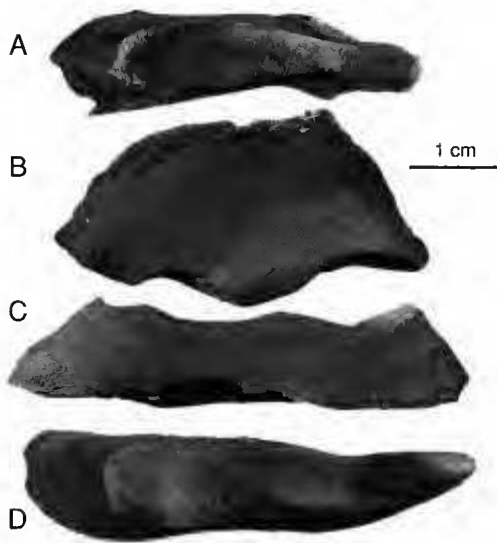


FIG. 10. — *Campbellodus decipiens* Miles et Young, 1977, WAM 95.6.112. A, B, upper toothplate, A, ventral view; B, mesial view; C, D, lower toothplate; C, mesial view; D, dorsal view. Whitened with ammonium chloride.

upper and lower toothplates (WAM 95.6.112) is shown here (Fig. 10), but adds no further information to the published description. The tooth plates had a crushing action with the posterior end of each tooth plate being broadest and thickest, and increased wear on the tooth plates result in differing morphologies, especially for the upper tooth plate, as noted by Miles & Young (1977: 150). A most peculiar feature of the dentition is that the lower toothplate extends anteriorly well forward of the anterior margin of the upper tooth plate when they occlude, as shown in the reconstruction (Fig. 6).

**Left quadrate.** (Figs 1K, 11) It is well-preserved in WAM 86.9.672. It is a robust perichondral ossified shell consisting of a main division with an inner flange, as described for *Austroptyctodus gardineri* (Miles & Young 1977, figs 24, 25). The main shaft is flat in cross-section with a broad articular end. Lateral to the articular surface (art.md) is a break in the perichondral bone surrounded by a thickening around it. This process (pr.det) is possibly a homologue with the “detent process” on the posterolateral region of the quadrate in arthrodires (e.g. *Goujetosteus pulchellus*, Gardiner & Miles 1990, fig. 20; *Menamarspis*, Long 1995b, fig. 16). This raises the question of

whether the “detent process” on the quadrate of ptyctodontids is actually homologous to that of arthrodires or corresponds to one of the several palatobasal articulations with the endocranium seen on the quadrate or palatoquadrate of other primitive placoderms (e.g. *Romundina*, Young 1986, fig. 12C). The function of the detent process in arthrodires is to limit movement or lateral slip of the jaw joint. This is clearly seen by physically moving the lower jaws and fixed cheek units against one another in well-preserved Gogo arthrodires. In acanthothoracids and thenanids, the palatobasal and nearby articulatory facets on the palatoquadrate were for attachment to the endocranium. In *Campbellodus* the quadrate is situated a considerable distance ventral to the extent of the braincase as deduced from similar positions of the endocranial ossifications and jaws in *Austroptyctodus* n.g., and thus the process in ptyctodontids is here seen to be homologous to the detent process in arthrodires, a constraint to lateral movement during opening and closing of the jaws. The large well-defined cavity for the posterior division of the adductor mandibulae muscles (add.foss) is seen in mesial view (Fig. 11B). The ventral surface of the quadrate (Fig. 11C) is relatively flat to weakly concave. It shows a roughened muscle or ligament attachment area (m.att) immediately anterior to the articulation area which may have been for the mandibulohyoid ligament.

The articular is not preserved in any of the *Campbellodus* specimens, but the autopalatine ossification is known from the holotype, and has been described and figured by Miles & Young (1977, fig. 11, pl. 2B).

#### Trunk shield

The trunk shield of *Campbellodus* (Figs 6, 12, 14) comprises large paired anterior lateral plates, paired anterior dorsolaterals, three median dorsal elements, the most distal of which is developed as a median spine, a pair of large interolateral plates, paired small spinal plates, and a small anterior median ventral plate. The restored trunk shield (Figs 6, 14) is similar to that of *Rhynchodus tetrodon* in having a very extensive branchial lamina on the anterior laterals and interolaterals with large hooked stellate tubercles,

but differs from all other known ptyctodontids in having three median dorsal bones, and distinctly small spinal plates.

**Median dorsal plates.** (MD1; Fig. 1H) Situated ventrally it straddles the anterior dorsolaterals and is a thin bone lacking a median ventral keel, as in *Rhamphodopsis*, *Chelyophorus*, *Ctenurella* and *Austroptyctodus* (e.g. Miles & Young 1977, fig. 29 D). It is the largest of the three dorsal trunk bones and has a strongly convex anterior margin that slightly overhung the nuchal gap of the head shield when the head was fitted onto the articulated trunk armour. It has a small dorsal overlap flange for the second median dorsal

plate (MD2; Fig. 1G). This plate is slightly more elongated than the main median dorsal, and also has a short, narrow overlap shelf on its postero-dorsal margin for the median dorsal spine. This spine (MD3; Fig. 1F) is similar to that figured by Miles & Young (1977, fig. 13) for specimen NHM P50907. It is a hollow bone with a grooved posterior face and has only few scattered tubercles on its surface, unlike the strongly developed dermal ornamentation in the spines of *Rhamphodopsis* and *Ptyctodopsis*.

**Anterior dorsolateral plate.** (ADL; Figs 12-14) It is of regular shape for ptyctodontids, not unlike that of *Ctenurella* or *Rhynchodus*. It has a well-

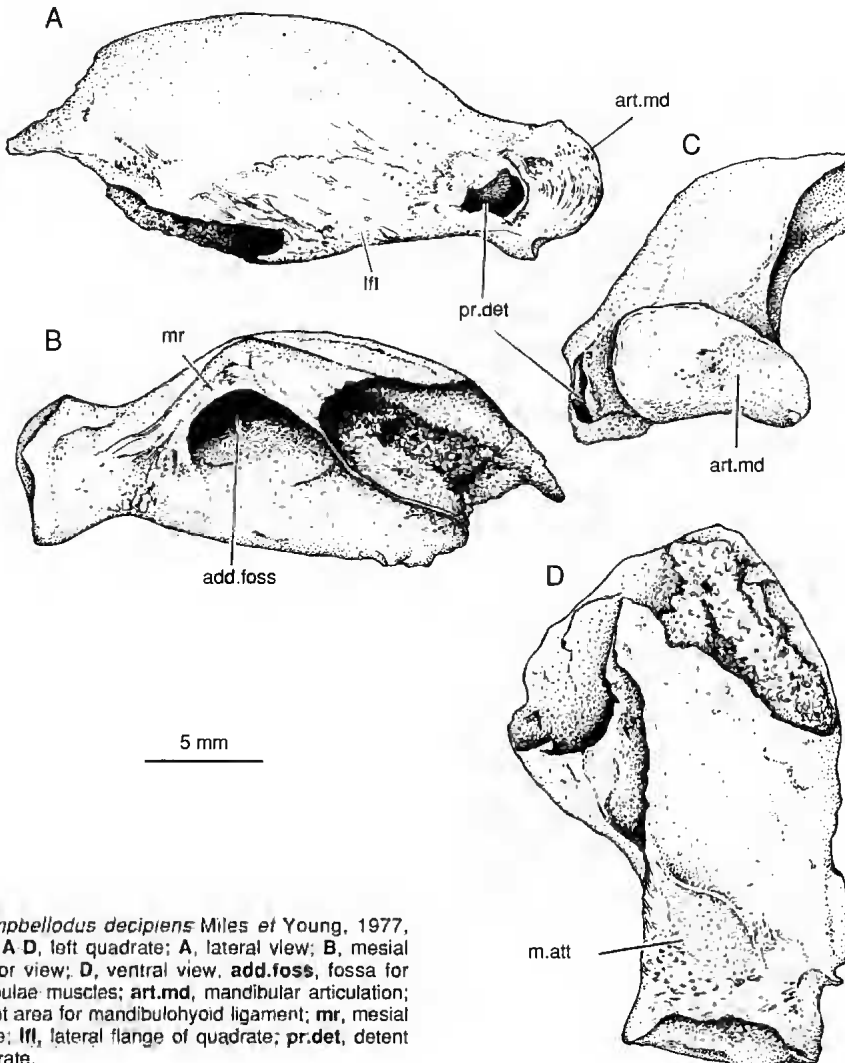


FIG. 11. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. A D, left quadrate; A, lateral view; B, mesial view; C, posterior view; D, ventral view. **add.foss**, fossa for adductor mandibulae muscles; **art.md**, mandibular articulation; **m.att**, attachment area for mandibulohyoid ligament; **mr**, mesial ridge of quadrate; **lfl**, lateral flange of quadrate; **pr.det**, detent process on quadrate.

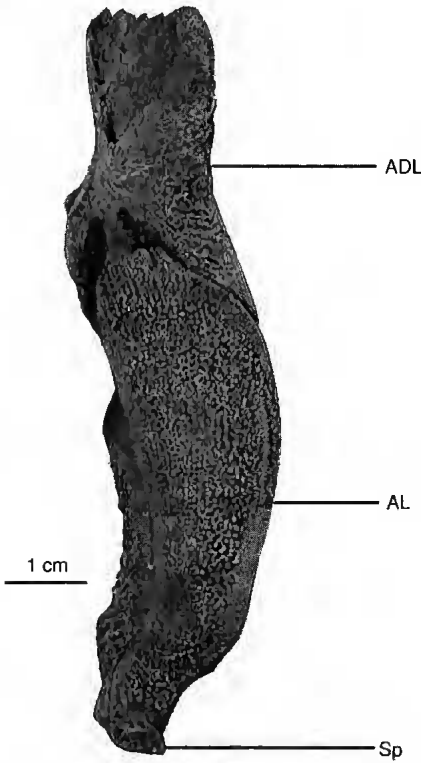


FIG. 12. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. Partially articulated trunk shield in left lateral view. ADL, anterior dorsolateral plate; AL, anterior lateral plate; Sp, spinal plate.

developed anterior ventral process of ornamented dermal bone that meets the anterior lateral plate (v.pr; Fig. 13), and the main lateral-line sensory canal (llc) passes through a tube within the bone and is not externally visible, nor is it expressed as a thickened tube on the visceral surface of the plate as occurs in ptyctodontid head shield bones. The articular condyle (art.con) for the neck joint is a broad flat surface with a weak median ridge which is hardly visible in lateral view (Figs 13, 14). Noticeable difference in the anterior dorsolateral plate of *Campbellodus* to those of other ptyctodontids is that it lacks the distinct angular inflection seen in the anterior dorsolateral plate of *Rhynchodus tetrodon* (Gross 1933, pl. 10, figs 2-4) or *Chelyophorus verneuili* (pers. obs.). It is broadest about two-thirds down its height from its dorsal margin, unlike the dorsally broader plate in *Austroptyctodus* (Miles & Young 1977, fig. 30), and the externally exposed region is noticeably

broader in its ventral division than in either *Ctenurella* or *Rhamphodopsis*. The overlap area for the median dorsal 1 plate (ov.MD) is much smaller than the large ventral overlap surface for the anterior lateral plate (ov.AL).

**Anterior laterals.** (AL; Figs 6, 12, 14) These are the largest bones of the dermal skeleton, as in all ptyctodontids. The dorsal region of the plate is very broad, being approximately three times the width of the narrow ventral division of the lateral lamina. The dorsal region of the anterior margin of the bone is strongly concave where the post-branchial lamina (Fig. 14, b. lam) begins. It has a well-defined lateral lamina with finely ornamented rugose dermal bone, merging mesially into the extensive flat postbranchial lamina covered with well-ordered rows of large, triangular pectinated tubercles. Each of these tubercles has a spray of about five or six inwardly pointed tips, the central one being the largest, and the head of the tubercles facing towards the centre of ossifi-

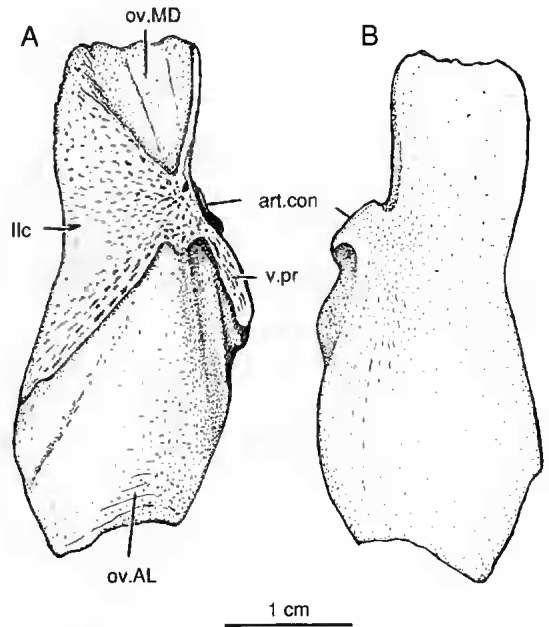


FIG. 13. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. A, B, anterior dorsolateral plate; A, right lateral view; B, mesial view. art.con, articular condyle or face on ADL plate; llc, main lateral line canal; ov.AL, overlap surfaces of anterior lateral plate; ov.MD, overlap surfaces of median dorsal plate; v.pr, ventral process of ornamented bone on anterior dorsolateral plate.



cation of the bone, close to its spinal margin. Miles & Young (1977, figs 1, 2F, pl. 4A) showed part of this postbranchial lamina on the type specimen, and figured a scanning electron micrograph showing clearly the morphology of one of these tubercles. The contact margin for the spinal plate is a short, straight horizontally-directed edge of bone above the embayed margin for the pectoral fin.

Unlike the condition in most other placoderms where the spinal plate projects anteriorly to the pectoral fin, it is clear that in *Campbellodus* the spinal plate is immediately dorsal to the main embayment in the trunk shield lateral lamina. The position of the scapulocoracoid in *Austroptyctodus*, also showing the fin emerged below the junction of the anterior lateral and the interolateral, confirms that the pectoral fin did emerge ventral to the position of the spinal in *Campbellodus*.

**Spinal plate.** (Sp; Figs 6, 12, 14) This small bone, with a very short projection of the posteriorly-facing spinal process, contacts the anterior lateral along almost all of its dorsal margin, but has only a very short anterior connection with the interolateral plate. In internal view, the spinal plate is hollow. It has been previously identified and described for the NHM P50907 by Miles & Young (1977, fig. 12).

**Interolateral plates.** (IL; Figs 6, 14) These consist mostly of the anteriorly facing postbranchial lamina, with no external lateral lamina. The ventral laminae (Fig. 14B) are well-developed as in all ptyctodontids and meet the anterior median ventral bone mesially, not contacting each other as occurs in *Rhynchodus tetrodon* (Gross 1933). As noted for the spinal, they have a well-defined pectoral incision for the pectoral fin (pec.in; Fig. 14A), and ventrally broaden out mesially. The postbranchial lamina has a strongly convex contact margin with the anterior lateral plates, similar to the condition in both *Rhynchodus* and *Austroptyctodus*.

**Anterior median ventral plate.** (AMV; Fig. 14 A, B) Unusually broad, it is more than twice as broad as its length, although its externally exposed surface in the articulated armour is very narrow. Most of its breadth is for the overlap laminae for the interolateral plates, and these surfaces have a fluted bone texture. The anterior margin of the plate is quite straight, unlike the V-shaped anterior median ventral plate in *Chelephorus*.

#### *Pelvic girdle and endoskeleton*

The pelvic girdles are well-preserved in the specimen showing two principal components, the dermal pelvic bones and associated endogirdle,

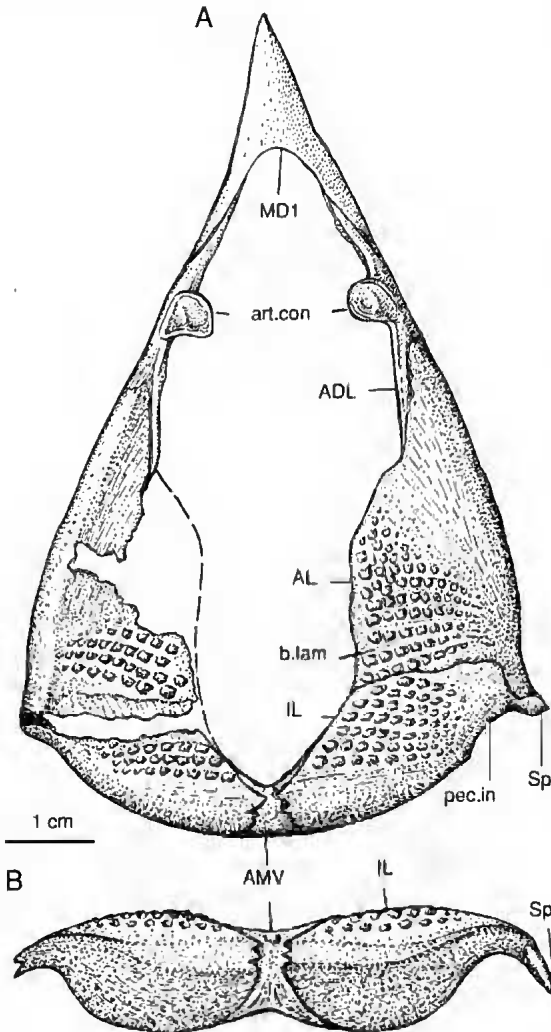


FIG. 14. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. A, B, trunk shield; A, anterior view; B, ventral view. ADL, anterior dorsolateral plate; AL, anterior lateral plate; AMV, anterior median ventral plate; art.con, articular condyle or face on ADL plate; b.lam, branchial lamina of trunk shield; IL, interolateral plate; MD1, median dorsal plate; pec.in, pectoral fin incision on trunk shield; Sp, spinal plate.

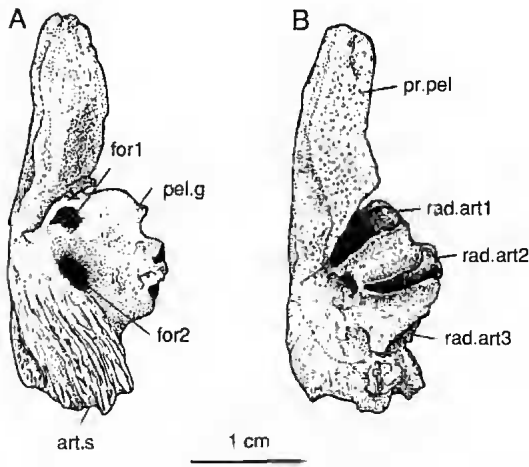


FIG. 15. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. **A, B**, prepelvic bone and associated endoskeletal pelvic girdle; **A**, dorsal view; **B**, ventral view. **art.s.**, articular scars for mesial attachment; **for.** for 1, 2, foramen or identified series of foramina; **pel.g.** groove between basal articulations on pelvic endoskeletal ossification; **pr.pel.** dermal process of pelvic girdle; **rad.art.** 1, 2, 3, articular facets for fin radials.

and a pair of asymmetric large, smooth basal plates for the pelvic fin, similar to the element described in the female specimens of *Rhamphodopsis threiplandi* (Miles 1967, figs 13, 15).

**External pelvic girdle.** (Figs 11, J, 15, 17) It has a large, narrow ventrolateral lamina with external ornament matching that of the dermal bones and scales. This part (**pr.pel**; Fig. 15) is probably equivalent to the paired prepelvic bones lying anterior to the pelvic fins in *Rhamphodopsis*, although the associated endoskeletal girdle is not known in that form. In the new specimen the perichondrally ossified endogirdle shows three large, elongated articulation surfaces for the pelvic fin radials (**rad.art** 1-3; Fig. 15), with two large foramina (**for** 1, 2) between the fin attachment surface and the outer dermal bone, for the passage of nerves, veins and arteries to the pelvic fin. Musculature of the pelvic fin probably attached to the roughened area surrounding these foramina and to the dermal component of the pelvic girdle. These paired elements met mesially by a roughened connection area (**art.s**) with an interdigitating suture (Fig. 17). The smooth surface surrounding this connective region was no doubt

covered with muscle or ligamentous connection in life. When the two parts of the pelvic girdle and endogirdle are reassembled in this way, the dermal prepelvic bones are not seen to have any mesial contact, as seen in *Rhamphodopsis*, but are widely separated. In restoring the pelvic girdle and endogirdles (Fig. 17), the bones were assembled with plasticine holding the basal plates together and then matched up with the posterior width of the trunk shield, so that the estimated width of the prepelvic bones correlated with the natural curvature of the body.

**Fin basal plate.** The large fin basal plate (Fig. 16) is represented by both left and right elements, although, as prepared, it is not known which is which. The element has strong curvature in both mesial-lateral direction and rostrocaudad, unlike in *Rhamphodopsis* specimens, in which it seems to be a flat, subtriangular bone. Along its inner ventral margin is a well-developed ridge (**ri**; Fig. 16A), presumably for inscription of the large pelvic scales along a broad, smooth flange (**fl**). A roughened area (**r.a**) is seen next to the centrally raised median area, presumably for attachment of ligaments and scales of the lateral flank of the fish. The visceral surface is smooth but has a

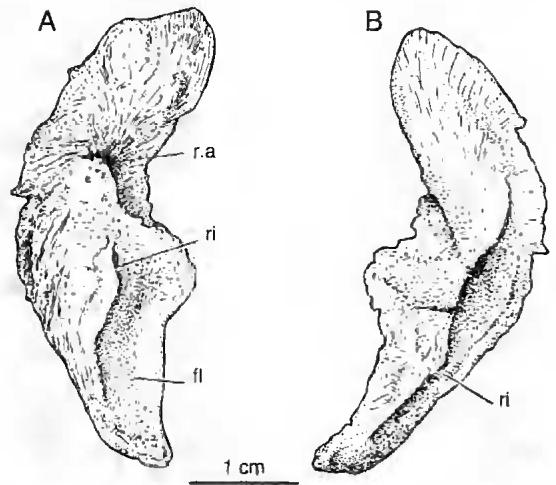


FIG. 16. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. **A, B**, right female pelvic basal plate; **A**, ventral view; **B**, dorsal view (slightly oblique, see figure 17 for possible orientation with respect to prepelvic bones and pelvic girdle). **fl**, flange; **r.a**, artulatory ridge on pelvic basal plate; **ri**, ridge for scale overlap on pelvic basal plate.

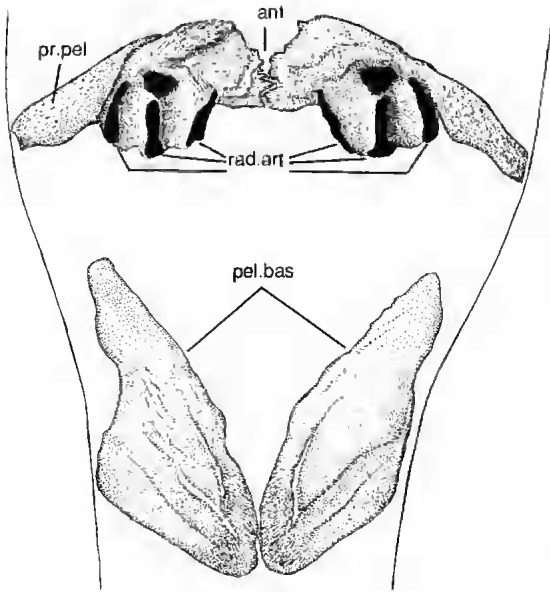


FIG. 17. — *Campbellodus decipiens* Miles et Young, 1977. Reconstruction of pelvic region of a female showing possible orientation of prepelvic bones, pelvic girdle and pelvic basal plates, ventral view; **ant**, anterior direction; **pel.bas**, pelvic basal bone (female basal ossification); **pr.pel**, dermal process of pelvic girdle; **rad.art**, 1, 2 articular facets for fin radials.

well-defined ridge (**ri**; Fig. 16B) running along its ventral lamina.

#### Scapulocoracoid?

A poorly preserved part of a perichondral ossification showing what appears to be a glenoid facet is here shown in figure 18 (**glen**), although,

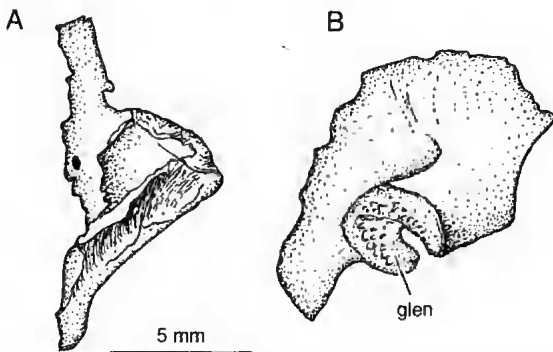


FIG. 18. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. Possible right scapulocoracoid ossification (incomplete). **glen**, glenoid condyle of endocranium.

as most of the bone is missing, its identification is uncertain. It is possibly part of the scapulocoracoid from the shoulder girdle, or alternatively may be a piece of the occipital ossification of the endocranium, as described below in *Austropryctodus*.

#### Axial skeleton

The vertebral column comprises the synarcual (Fig. 19) and numerous paired perichondral elements that straddled the cartilaginous notochord, as described for *Rhamphodopsis* (Miles 1976), *Ctenurella gladbachensis* (Ørving 1960), and similar to the vertebral ossifications seen in other placoderms (e.g. *Coccosteus*, Miles & Westoll 1968; *Austrophyllolepis*, Long 1984b; *Incisoscutum*, Dennis-Bryan & Miles 1981; *Eastmanosteus*, Dennis-Bryan 1987). Some of the haemal arch elements have reasonably long ventral processes compared to those seen in *Ctenurella* or *Rhamphodopsis*.

**Synarcual.** It is similar to that described for *Austropryctodus* (Miles & Young 1977, fig. 32), showing clearly the notochordal groove (**not.gr**; Fig. 19) canal for the spinal cord (**sp.c**) and lateral

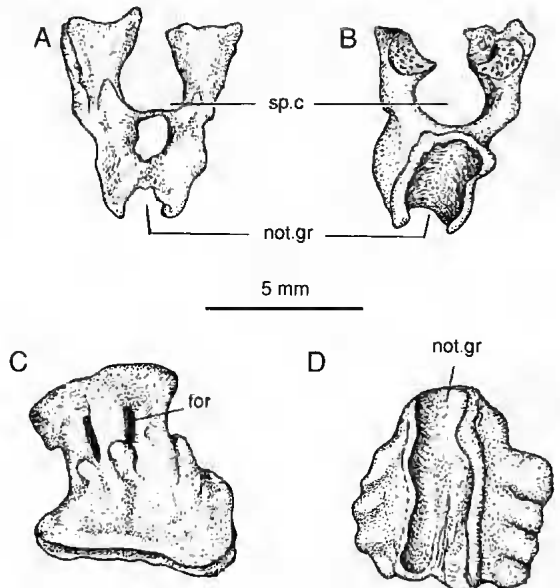


FIG. 19. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. **A-D**, synarcual; **A**, anterior view; **B**, oblique posterior view; **C**, lateral view. **D**, ventral view. **for**, foramen or identified series of foramina; **not.gr**, notochordal groove; **sp.c**, spinal cord canal.

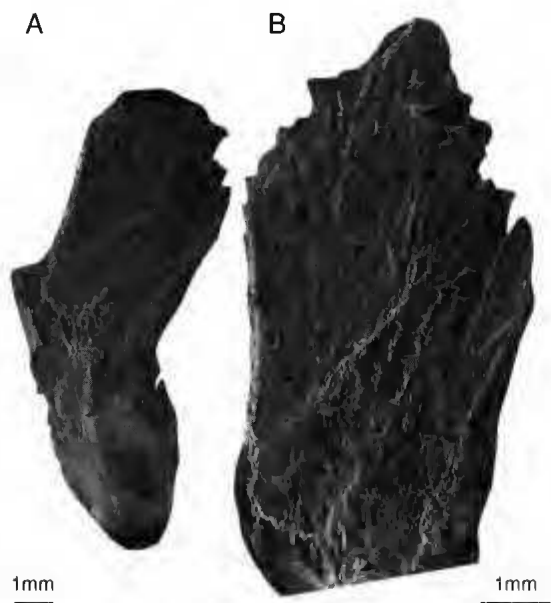


FIG. 20. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. **A**, dermal scale showing overall shape; **B**, detail of externally ornamented area of same scale. SEM photomicrographs.

slit-like foramina (for) for the spinal nerve roots. Large basal elements for the median fins are found in the material and in general outline match those described for *Austroptyctodus* (Miles & Young 1977, figs 33, 34). In addition there is a posteriorly situated second median dorsal bone that bears a close resemblance to the median dorsal 1 of the trunk shield. As for *Ctenurella gladbachensis*, this is presumed to be the dorsal spine preceding the second dorsal fin.

#### Squamation

The specimen contained many hundreds of scales distributed throughout the nodule, and not concentrated specifically around the pelvic girdle. Thus, as in the articulated specimen of *Austroptyctodus* described below, in which ordered scale rows are seen on the flank of the trunk region, the whole of the body posterior to the trunk shield is assumed to have been covered by large overlapping scales. Each scale has an ornamented external region which is subrectangular in form but quite variable as to precise shape (Figs 20, 21) and a large, ventrally-facing smooth overlap surface. The scales are macromeric, from

their large size and the relative size of the neural arch elements it is suggested that there was a correspondence of one scale row per somite, and that they were ordered in neat rows with large overlapping ventral flanges.

Long (1995b: 110) gives an attempted life restoration of *Campbellodus decipiens* based on the new material described herein.

## REVISION OF THE GENUS

### *Ctenurella* Ørvig, 1960

Although the original description of *Ctenurella gladbachensis* by Ørvig (1960) did not recognise the presence of the submarginal bone, this was soon corrected along with further observations of the material by him (1962). Another peculiarity of *C. gladbachensis* noted from Ørvig's description is the purported absence of the anterior median ventral plate, present in all other ptyctodontids where the armour is well-preserved, including *C. gardineri* (Miles & Young 1977, fig. 31). His last reconstruction of the head of *C. gladbachensis* was modified to show broader anterior margins on the preorbital plates and was subsequently adopted by Stensiö (1969, fig. 40A) and used by Ørvig (1971) and Miles & Young (1977, fig. 15). It incorporated a smaller dermal bone anterior to the marginal plate (a possible suborbital bone).

Denison (1978, fig. 3B) attempted to reconstruct parts of the visceral skeleton of *C. gladbachensis*, adding the hyomandibular as an anteroventrally directed bone, bracing the jaw articulation and meeting with an opercular cartilage. Forey & Gardiner (1986) described a new specimen of the Gogo "*Ctenurella*" and figured newly prepared NMH specimens of *C. gladbachensis* in which the "ceratohyal" was clearly identified.

Original specimens in the MNHN, Paris, include articulated individuals showing details of the skull roof, jaws and visceral skeleton (Fig. 22) and one superb specimen, both part and counterpart (Figs 23, 24B, 25), meticulously prepared by Dr. D. Goujet, showing the dermal bones of the skull and trunk shield, as well as jaws and associated ossifications, the hyoid elements, ros-

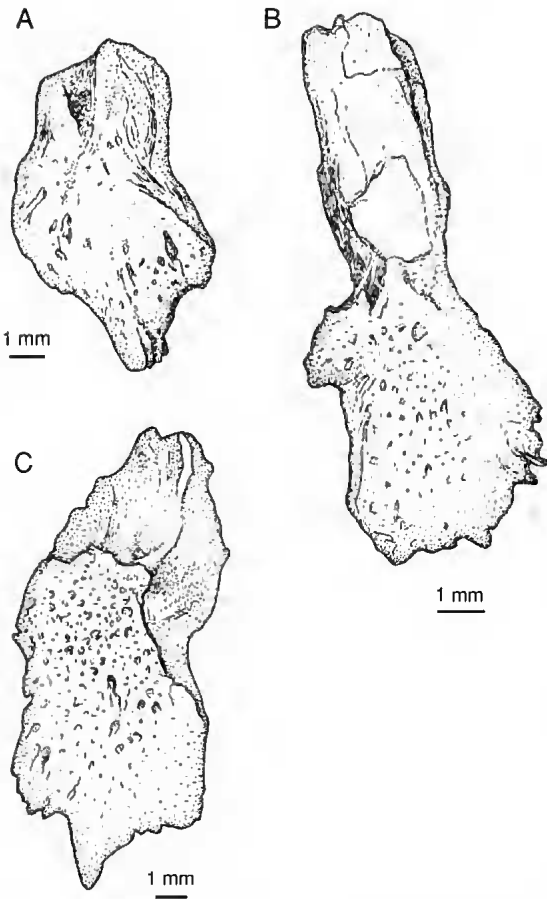


FIG. 21. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. Dermal scales. A, basal view; B, C, coronal views.

tral cartilages and other visceral arch elements. Four well-preserved specimens were studied in order to determine the nature of the hyoid arch bones, the jaw cartilages and the reconstruction of the head shield. The new specimens examined at the MNHN, Paris, corroborate the orientation of the interhyal bone, as observed by Forey & Gardiner (1986, called the "ceratohyal") in its posteroventrally slanted position behind the articular, as seen also in *Austroptyctodus* (Figs 28, 29). Closer examination reveals that the expanded head of the interhyal in *C. gladbachensis* only makes contact with the posterior margin of the articular and does not meet with the posterior edge of the quadrate (Fig. 25).

The skull roof is well-preserved in the NHM

specimens but differs in several respects from the reconstructions given by Ørvig (1960, 1971), Stensiö (1969), Miles & Young (1977) and Denison (1978). In all four of the NHM specimens examined, the central plates meet each other behind the nuchal plate, unlike the condition in both the Gogo ptyctodontids, in which the nuchal forms the median posterior margin of the head shield (Figs 23, 25B). The anterior margin of the head shield is relatively broad and straight with the pineal bone tightly enclosed by the anteromesial corners of the preorbital plates. The closure of the central plates to form the posterior margin of the head shield in *Ctenurella gladbachensis* is also hinted at in the one skull figured by Ørvig (1960, pl. 26, 1, 2) where the left central plate protrudes behind the nuchal plate. The pineal plate is always firmly enclosed by the preorbital plates with only a short anterior margin forming the anterior border of the head shield, unlike the Gogo form which has a pineal plate significantly smaller than the gap defined for it by the preorbitals.

Thus, a new reconstruction of the skull roof of *Ctenurella gladbachensis* is presented here (Fig. 26B) which shows noticeable differences to the Gogo specimens.

It is noted that the sclerotic ring, not previously described for ptyctodontids, is well preserved in one Bergisch-Gladbach specimen, and shown clearly in figure 22A (bottom right corner above the lower tooth plate). It comprises four sclerotic bones and matches closely with the supraorbital vault defined by the preorbital and postorbital plates.

The lower tooth plates of *Ctenurella gladbachensis* have a well-developed ventral process (Figs 22A, 25), a feature also seen in the Gogo *Austroptyctodus* (Fig. 34; Miles & Young 1977, pl. 5B). Further differences between *Ctenurella* and *Austroptyctodus* are seen in the median dorsal plates. In *Ctenurella* (Fig. 22A) it has weakly convex lateral margins and the posterior margin even has a taper to a posterior point. In *Austroptyctodus*, the median dorsal plate has a much broader anterior margin than its posterior margin, weakly concave lateral margins and a more strongly developed posterior process (Miles & Young 1977, fig. 29D).

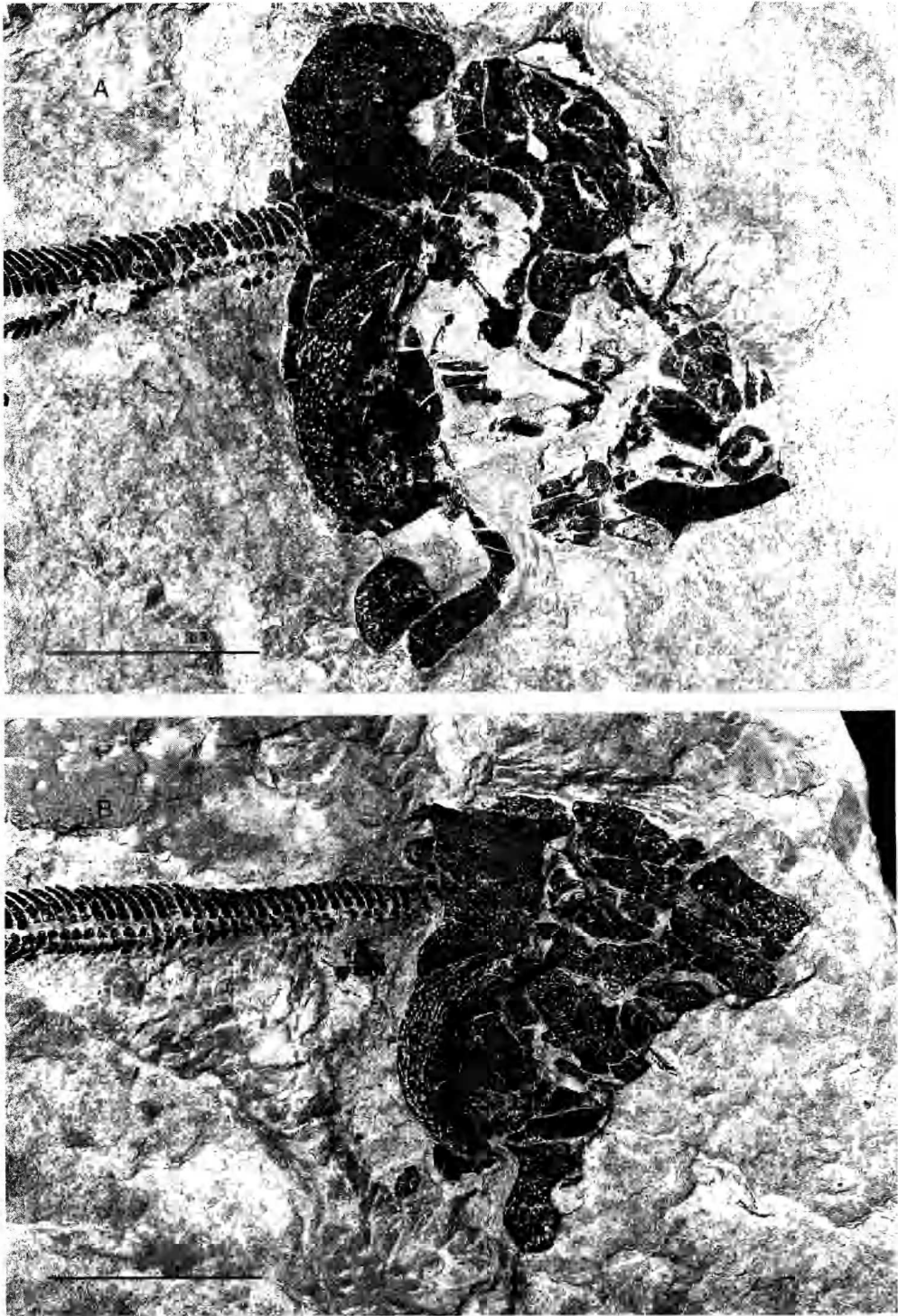


FIG. 22. — *Ctenurella gladbachensis* Ørvig, 1960. Specimens in the palaeontological collections of the Muséum national d'Histoire naturelle, Paris. **A**, MNHN ARD 229, note presence of small sclerotic ring near lower jaw tooth plate, **B**, MNHN ARD 231. Scale bar: 1 cm.





FIG. 23. — *Ctenurella gladbachensis* Ørvig, 1960. Specimens in the palaeontological collections of the Muséum national d'Histoire naturelle, Paris. **A**, MNHN ARD 230; **B**, MNHN ARD 233. Scale bar: 1 cm.

AMENDED GENERIC DIAGNOSIS

A small ptyctodontid with a nuchal completely enclosed by the centrals and preorbitals; preorbitals meet in midline and suture with the pineal; nuchal plate anteriorly pointed. Marginal plates with well-developed ventral process. Toothplates of the shearing type, lower tooth plates having a well-developed ventral process near the articular end. Trunk shield lacking a spinal plate, median dorsal plate approximately as broad as long, lacking a dorsal spine, and with lateral margins gently convex. Body lacking squamation.

REMARKS

The genus *Ctenurella* is distinguished from *Rhynchodus*, *Rhamphodopsis*, *Ptyctodopsis*, *Tolloodus* and *Campbellodus* by its absence of a spinal plate. *Chelyophorus* differs in having grooves developed for the external sensory-line system, a shorter, broader nuchal plate and higher, shorter anterior dorsolateral plate. *Austroptyctodus* n.g. is distinguished by its skull-roof pattern, with nuchal plate opened, posteriorly, the different shape of the median dorsal plate and the presence of body scale cover.

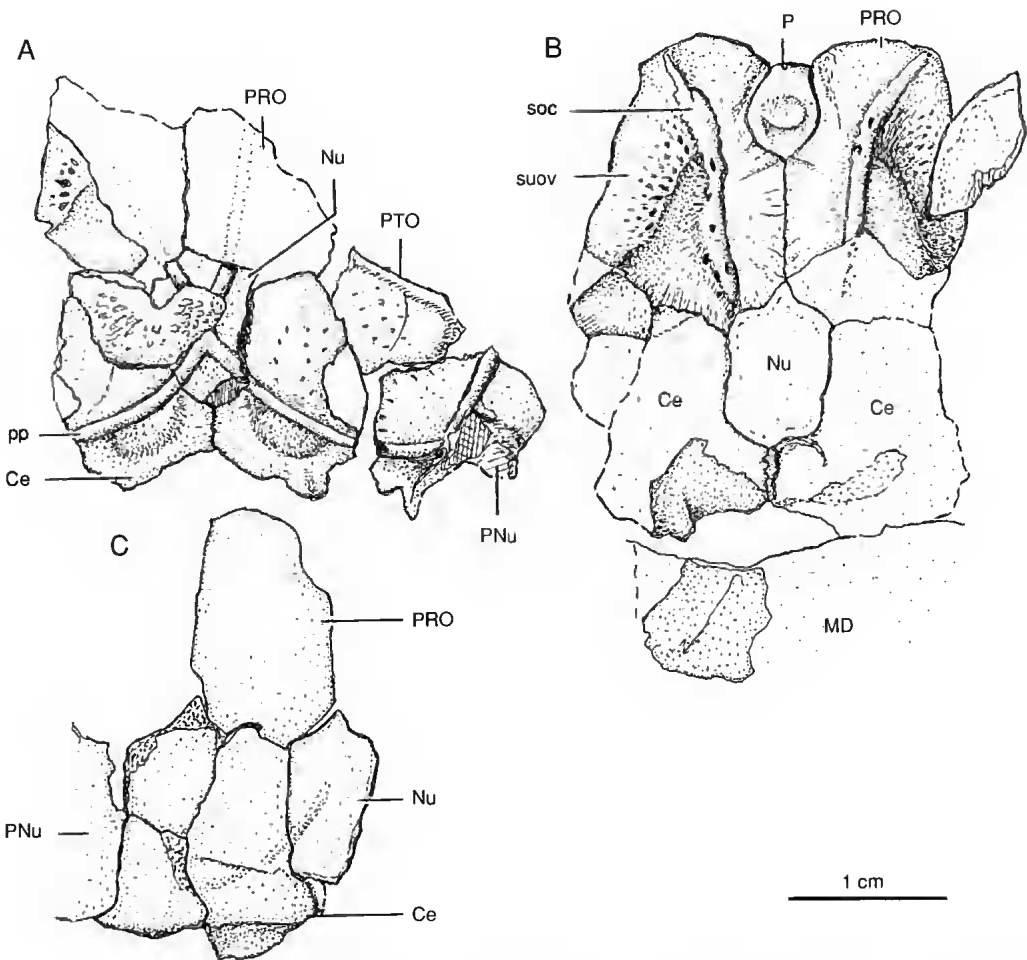


FIG. 24. — *Ctenurella gladbachensis* Ørvig, 1960. Sketches of specimens showing head shield plates in articulated position. **A**, MNHN ARD 233; **B**, MNHN ARD 230b; **C**, MNHN ARD 232. **Ce**, central plate; **MD**, MD1, 2, 3, median dorsal plate(s) or spines; **Nu**, nuchal plate (posterior element), **P**, pineal plate or space provided for it in the head shield; **PNu**, paranuchal plate; **pp**, posterior sensory-line canal on head shield; **PRO**, preorbital plate; **PTO**, postorbital plate; **soc**, supraorbital sensory-line canal; **suov**, supraorbital vault.

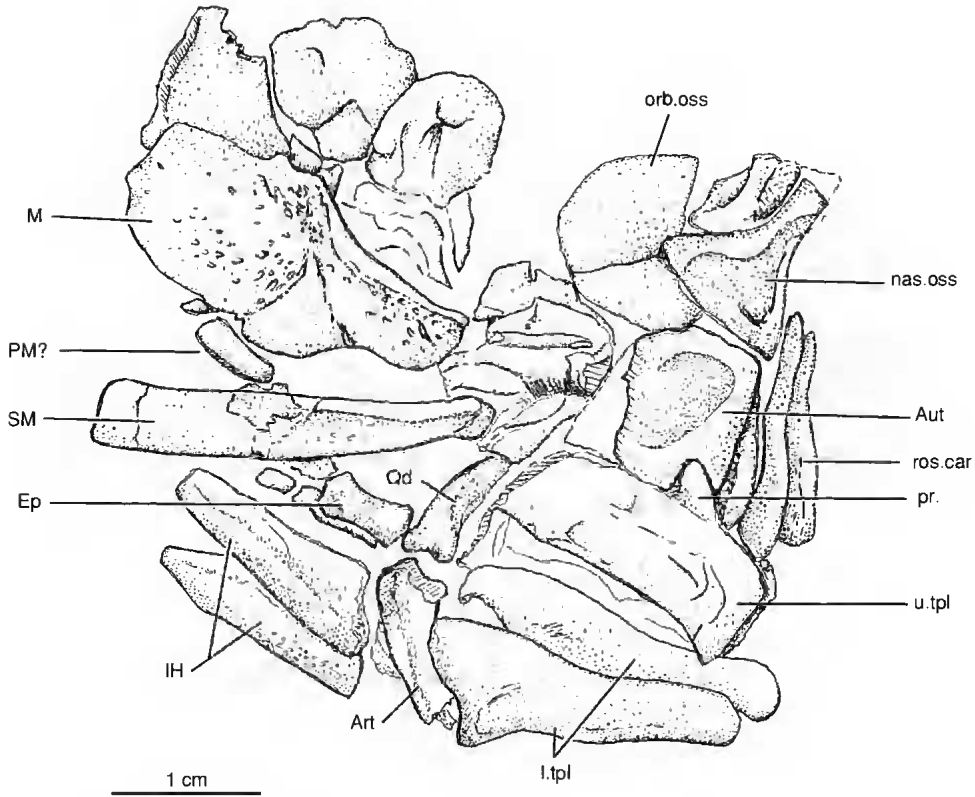


FIG. 25. — *Ctenurella gladbachensis* Ørvig, 1960. Sketch of specimen MNHN ARD 229 (as shown photographed in figure 22). **Art**, articular; **Aut**, autopalatine; **Ep**, epibranchials; **IH**, interhyal element; **l.tpl**, lower tooth plate; **M**, marginal plate; **nas.oss**, nasal ossification of endocranium; **orb.oss**, orbital ossification of endocranium; **PM**, postmarginal plate; **pr.**, dorsal process of the upper tooth plate; **Qd**, quadrate; **ros.car**, rostral cartilages (paired); **SM**, submarginal plate; **u.tpl**, upper tooth plate.

*Austroptyctodus gardineri*  
(Miles et Young, 1977) n.g.  
*Austroptyctodus* n.g.

TYPE SPECIES. — *Austroptyctodus gardineri* Miles et Young, 1977.

ETYMOLOGY. — From the continent Australia and the form genus *Ptyctodus*.

DIAGNOSIS. — A ptyctodontid placoderm having a *Ptyctodus*-like crushing dentition, preorbital plates separated from each other by a median gap. Canal-bearing nuchal participating in the posterior margin of the skull roof, trunk shield lacking a spinal plate, median dorsal plate with much wider anterior margin than posterior margin. The body was covered by large overlapping scales.

REMARKS. — *Austroptyctodus* n.g. is clearly distinguished from all other well-known ptyctodontids (*i.e.* those

known from most of the dermal armour) except *Ctenurella* and *Chelyphorus*, in lacking a spinal plate. It is distinguished from *Ctenurella* by several features noted above under "Remarks" for *Ctenurella gladbachensis*.

*Austroptyctodus gardineri*  
Miles et Young, 1977

*Ctenurella gardineri* Miles et Young, 1977. — Denison 1978: 29. — Long 1984a: fig. 171-L. — Forey & Gardiner 1986: fig. 2. — Long 1991: 366, fig. 20I, 377.

HOLOTYPE. — WAM 70.4.253, previously described and figured by Miles & Young (1977, pl. 2D, E, pl. 3B, pl. 4B) with the provisional Natural History Museum number for the specimen (P.57637).

OTHER MATERIAL. — NHM, London: P50906,

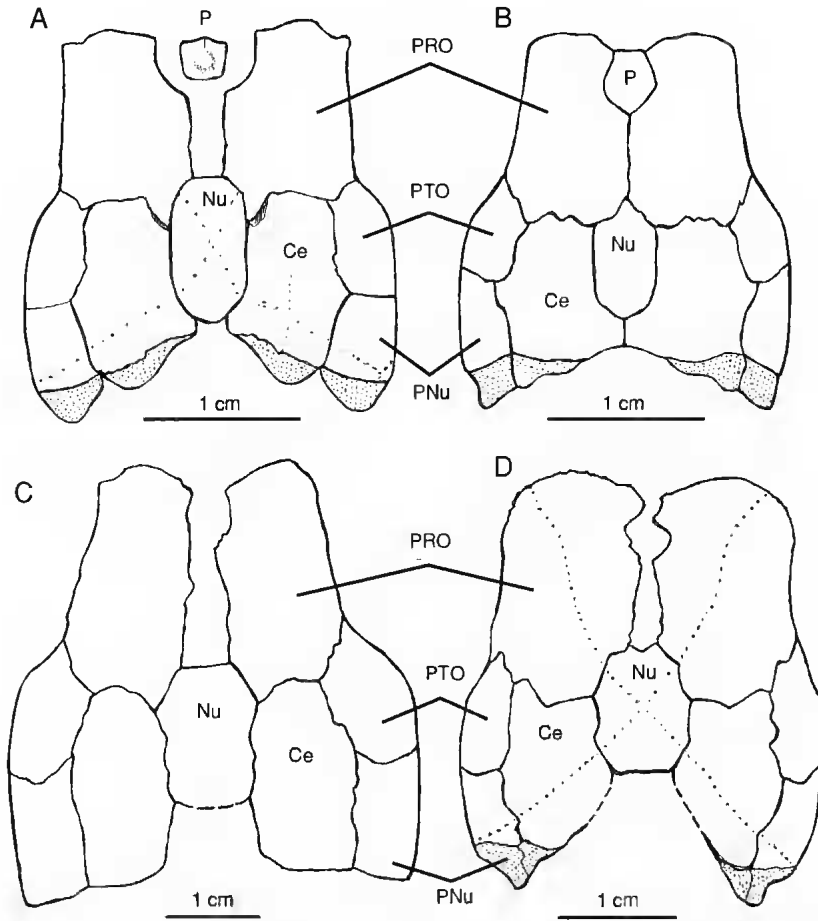


FIG. 26. — Comparison between the reconstructed head shields in dorsal view: A, *Austroptyctodus gardineri* (Miles et Young, 1977) n.g.; B, *Ctenurella gladbachensis* Ørvig, 1960; C, *Rhynchodus tetradon* (after the Holotype); D, *Campbellodus decipiens* Miles et Young 1977. Ce., central plate; Nu, nuchal plate (posterior element); P, pineal plate, or space provided for it in the head shield; PNu, paranuchal plate; PRO, preorbital plate; PTO, postorbital plate.

P50908, P50909, P50910, P57654, P57655; WAM 86.9.662.

DESCRIPTION

The new Gogo specimen of *Austroptyctodus gardineri* (WAM 86.9.662, Figs 27-29) was collected by the author in August 1986. It is an almost complete specimen preserved as far posteriorly as approximately the middle of the main dorsal fin. It has been prepared by the resin transfer method for both part and counterpart. As Miles & Young (1977) have already described in detail most of the dermal skeleton in this form, the following description focuses only on new information,

and provides new reconstructions for the dermal skull roof and visceral skeleton, and external armour in lateral view.

*Skull roof and cheek*

The skull roof was not reconstructed by Miles & Young (1977, 157) as they stated that “several problems were encountered in attempting to reconstruct the skull-roof from the accurately known shape of individual bones”. The new knowledge of the skull roof of *Campbellodus* presented above shows there is not a close fit between all skull roof bones. Earlier, inaccurate reconstructions of the skull roof of *A. gardineri*

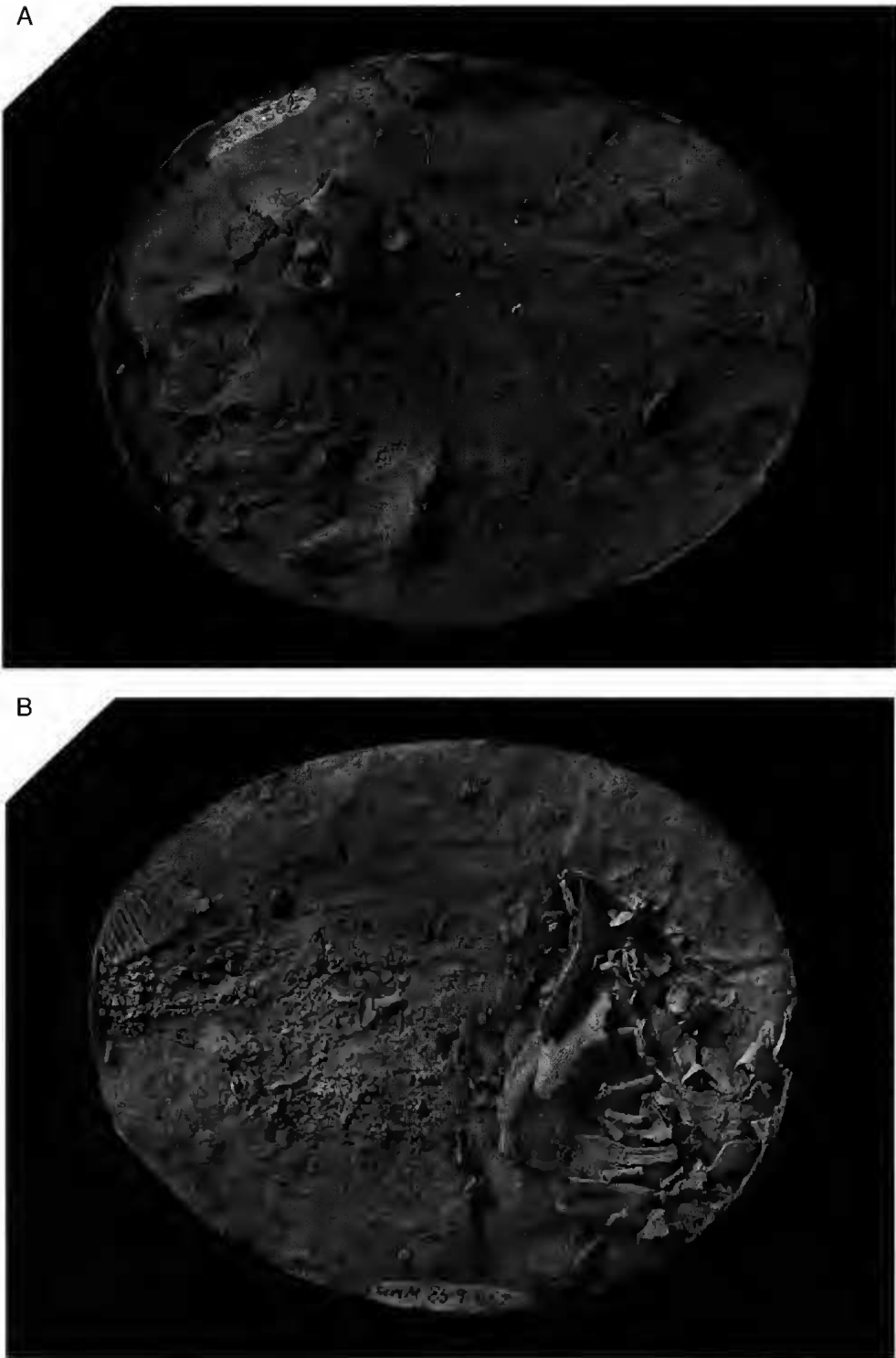


FIG. 27. — *Austroptyctodus gardineri* (Miles et Young, 1977) n.g. WAM 86.9.662, showing both sides of specimen embedded in resin, whitened with ammonium chloride. Natural size.



FIG. 28. — *Austroptyctodus gardineri* (Miles et Young, 1977) n.g. WAM 86.9.662, showing details of internal ossifications of the head and part of right side of trunk shield. Whitened with ammonium chloride. See figure 29 for scale.



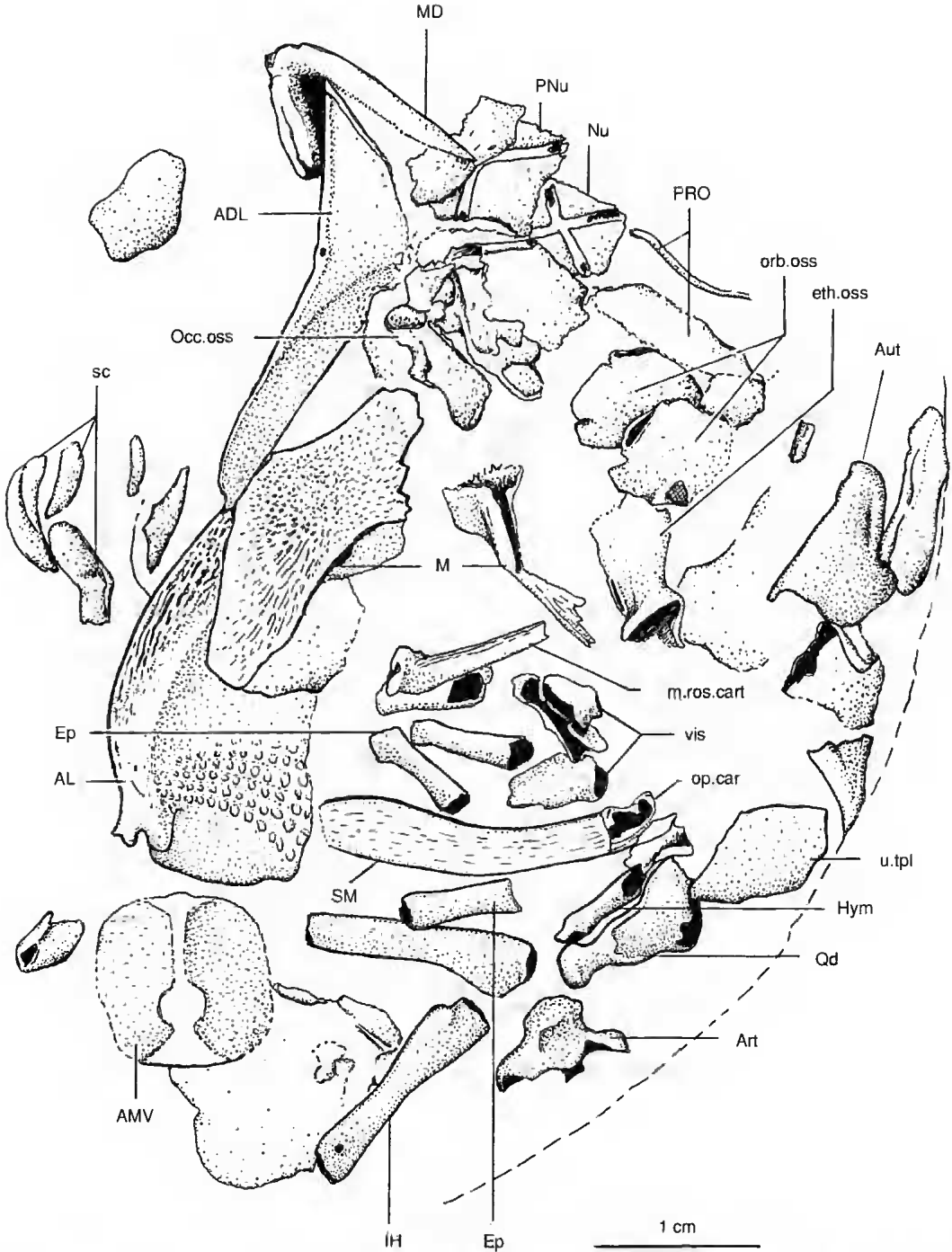


FIG. 29. — *Austroptyctodus gardineri* n.g. (Miles *et* Young, 1977). WAM 86.9.662, sketch interpretation (see figure 27). **ADL**, anterior dorsolateral plate; **AL**, anterior lateral plate; **AMV**, anterior median ventral plate; **Art**, articular; **Aut**, autopalatine; **Ep**, epibranchials; **eth.oss**, ethmoid ossification of endocranium; **Hym**, hyomandibular; **IH**, interhyal element; **M**, marginal plate; **MD**, MD1, 2, 3, median dorsal plate(s) or spines; **m.ros.cart.**, median rostral ossification; **Nu**, nuchal plate (posterior element); **Occ.oss**, occipital ossification of endocranium; **op.car.**, opercular cartilage; **orb.oss**, orbital ossification of endocranium; **PNu**, paranuchal plate; **PRO**, pre-orbital plate; **Qd**, quadrate; **sc**, scales; **SM**, submarginal plate; **u.tpl**, upper tooth plate; **vis**, "visceral skeleton elements?".

were given by Long (1984a, 1991), made by fitting these bones together from sketches. When the bones of one individual are accurately assembled (e.g. P57637, WAM 86.9.662), the skull roof closely resembles that of *Campbellodus* in having a median gap between the preorbitals. The pineal plate is actually smaller than the notch as defined for it by the associated preorbital plates (Fig. 26A), as noted by Miles & Young (1977). The visceral surface of the skull roof shows only weak development of the supraorbital vault, without substantial development of an inwardly projecting lamina from the orbital rim, as seen in *Campbellodus*.

The marginal and submarginal plates were well described by Miles & Young (1977). There is no evidence of a smaller postmarginal bone, as suggested to be present in *Ctenurella gardineri* by Ørvig (1970, although this observation is not confirmed by the present study).

#### Visceral skeleton

As discussed above for *Campbellodus*, the evidence from specimens of *Ctenurella gladbachensis* suggests that the hyoid arch was well-ossified with an expanded interhyal element posteriorly extended to provide an extra attachment region for a flexible opercular membrane. This element was identified as the "ceratohyal" by Forey & Gardiner (1986), and is here shown in various views (Fig. 30). It has two articular heads proximally where it meets the articular and the hyomandibular dorsally (as in *Ctenurella*, Fig. 25). The broad, inwardly curved ceratohyal which is found in *Campbellodus* has not been positively identified in the *Austroptyctodus* material. It was probably not preserved in WAM 86.9.662 as the anterior region of the head is missing, including the lower tooth plates.

**Opercular cartilage and hyomandibular.** (op.car; Fig. 29) It is found on the inside of the head of the submarginal as in all other placoderms where it is preserved (see Young 1986, for a review of the distribution of this structure). This structure was identified in *Austroptyctodus* by Forey & Gardiner (1986, fig. 1B) as the hyomandibular, and restored as having an enclosed, tubular head. In *Campbellodus*, the corresponding ossification is broader, with an extensive

ventral lamina. There is no evidence that it was an elongate element, and a large cartilage structure that acted as the flexible gill-cover has been restored (Fig. 6). WAM 86.9.662 gives further support for interpreting this as an opercular cartilage rather than as an epihyal, as the hyomandibular is seen *in situ*, lying immediately dorsal to the quadrate (Hyni; Figs 28, 29). The proximal head of the hyomandibular is not preserved but it terminates in close proximity ventral to the opercular cartilage, presumably meeting the anterior postorbital process of the braincase (a perichondral shell inside the marginal plate), just forward of the centre of the orbital cavity, as it does in *Brindabellaspis* (Young 1980).

#### Endocranium

Endocranial ossifications in ptyctodontids were first noted by Eichwald (1859, pl. 57, fig. 1) in a well-preserved specimen of *Chelephorus verneuili*, in which two pairs of roughly circular ossifications were found in the articulated head, below the occipital region and underneath the orbits. This specimen has now been acid prepared to confirm the placement of these ossifications (Dr. A. Ivanov, pers. comm. 1995). Ørvig (1962, 1971) observed perichondrally ossified laminae in the orbital regions of the Bergisch-Gladbach *Ctenurella* specimens, and Miles (1967: 105a) confirmed the presence of a small semi-circular bone in the orbital region of *Rhampadopsis*, previously alluded to by Watson (1938).

Miles & Young (1977) gave the first detailed description of the endocranial components of ptyctodontids based on the Gogo specimens of *Austroptyctodus*. They identified at least three pairs of perichondrally-ossified bones which they termed (1) the occipital ossification, (2) the orbital ossification, and (3) the ethmoid ossification. Although various foramina were described on these ossifications, their outlines were not completely clear and so they were only given approximate correlations with the landmark foramina known on the braincases of other placoderms. They further stated that the exact arrangement and relationship of these endocranial ossifications within the articulated head were not clear at all. The new specimen described here gives more precise information on the morphology,

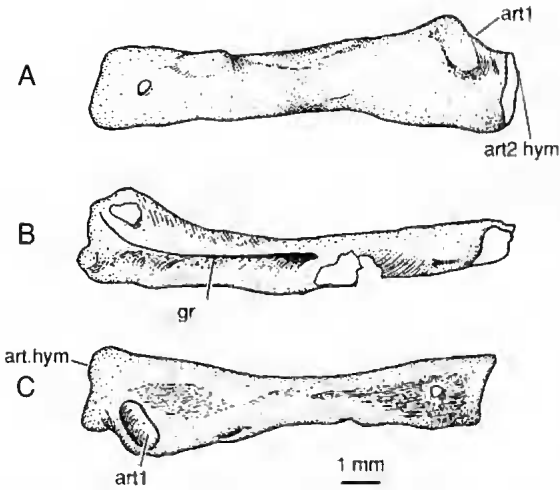


FIG. 30. — *Austroptyctodus gardineri* (Miles et Young, 1977) n.g. WAM 86.9.662, right interhyal bone; A, C, lateral views; B, dorsal view. art, articulation facets for hyomandibular; art.hym, articulation for hyomandibular; gr, groove.

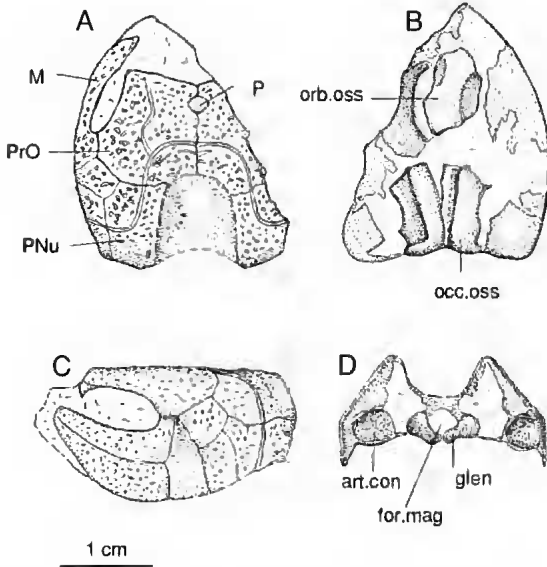


FIG. 31. — *Chelyophorus verneuili* Agassiz, 1844. Articulated specimen, redrawn after plate 57, fig. 1 of Eichwald (1859). A, head shield in dorsal view; B, head in ventral view showing orbital and occipital ossifications of braincase; C, head shield in left lateral view; D, posterior view of head showing glenoid condyles of braincase and articular flange of paranuchal plates. art.con, articular condyle or face on ADL plate; for.mag, foramen magnum of endocranium; glen, glenoid condyle of endocranium; M, marginal plate, occ.oss, occipital ossification of endocranium; orb.oss, orbital ossification of endocranium; P, pineal plate or space provided for it in the head shield; PNu, paranuchal plate; PrO, preorbital plate.

position and contact relationships of these elements and can be corroborated by new observations on the endocranial ossifications examined in both *Chelyophorus verneuili* and *Ctenurella gladbachensis*. Recently prepared material of a new genus of ptyctodontid from the Late Devonian Gneudna Formation of Western Australia also shows the occipital and orbital ossifications perfectly preserved in 3-dimensional form, corroborating the foramina and morphological features with those preserved in other ptyctodontids.

Three paired ossifications of the endocranium of *Austroptyctodus* are preserved in WAM 86.9.662 (occ.oss, orb.oss, eth.oss; Figs 28, 29), all in close association and only displaced slightly from articulated position, as supported by the close articulation of the other neighbouring dermal bones. A fourth pair of bones lies dorsal to the palatoquadrate which precede the nasal capsules. These have been labelled as "metapterygoids" in previous descriptions. There are also perichondral conical shells of bone attached to the inside wall of the marginal plate that contacted the orbital ossifications laterally. These are here assumed to have housed the posterior postorbital process, as for other placoderms (Young 1979, 1980, 1986; Lelievre 1995).

The presumed position of the posterior three of these paired endocranial ossifications, with relation to the dermal exocranium, was proposed by Miles & Young (1977, fig. 22) who correctly positioned the occipital bones but restored the orbitals as oriented with their flat lamina vertically. They did not attempt to place the ethmoid ossification in relation to the skull roof, but noted that its large anterior articulation facet was most likely an articulation to the autopalatine, as also pointed out by Young (1986). Evidence from the new specimen (Fig. 28) shows an alignment of the occipital, orbital and ethmoid bones, each part only slightly displaced from its antimer. The assumed fit of these bones is in line forming the ventral wall of the endocranium, as shown by *Chelyophorus verneuili* (Fig. 31, redrawn from Eichwald 1859) and in several specimens of *Ctenurella gladbachensis* in which the paired orbital ossifications remain articulated mesially, usually found in close proximity to the

orbits (as it also occurs in the holotype of *Austroptyctodus*, WAM 70.4.253). Other specimens of this species show the ethmoid articulation in the anteroventral corner of the orbit, closely associated with the autopalatine and metapterygoid, and with the head of the submarginal bone snuggled into a depression immediately behind its large articulatory facet. Thus, from these various specimens it is now possible to redescribe and accurately reconstruct the endocranium in *Austroptyctodus*, and to discuss the homology of parts of its structure to that in other placoderms.

#### Occipital ossification

The occipital ossification was well described by Miles & Young (1977, fig. 20), although the margins of their specimen were not well-preserved enough to show its complete shape. In *Austroptyctodus* (WAM 86.9.662), as well as in *Chelephorus* and in the new *Gneudna* ptyctodontid, the occipital ossifications are well-preserved and show their complete outlines. The material largely supports the reconstructions of Miles & Young (1977), showing that the ventral lamina of this bone possessed a large groove (gr. dla; Fig. 32C) that presumably carried the dorsolateral aorta, with each side carrying the groove anterolaterally away from the glenoid condyles. In lateral view (Fig. 32A), there are three large foramina visible and the outer damaged part of the ascending occipital process (pr.oc; Fig. 32 A) reveals that there was a hollow tube in the outer wall of the ossification, probably opening in the position where Miles & Young (1977, fig. 20C) observed a slit in the endocranial wall. The anterior two of these large foramina in the lateral wall of the occipital ossification (Fig. 32A, B, for 2, 3) were tentatively identified as for the vagus and glossopharyngeal nerves by Miles & Young. This interpretation would seem correct by comparison with the foramina found in the similar region of lateral endocranial wall occupied by other known placoderms (e.g. *Brindabellaspis*, Young 1980; *Dicksonosteus*, Goujet 1984a; *Macropetalichthys*, as reinterpreted by Young 1986). There is also a large ventral slit containing a foramen lateral to the glenoid process (Fig. 32A, for), also recognised by

Miles & Young (1977, fig. 20, c1, sl). As this opening is posteriorly directed and not confluent with the pathway for the dorsolateral aorta, it may possibly represent the path of the occipital

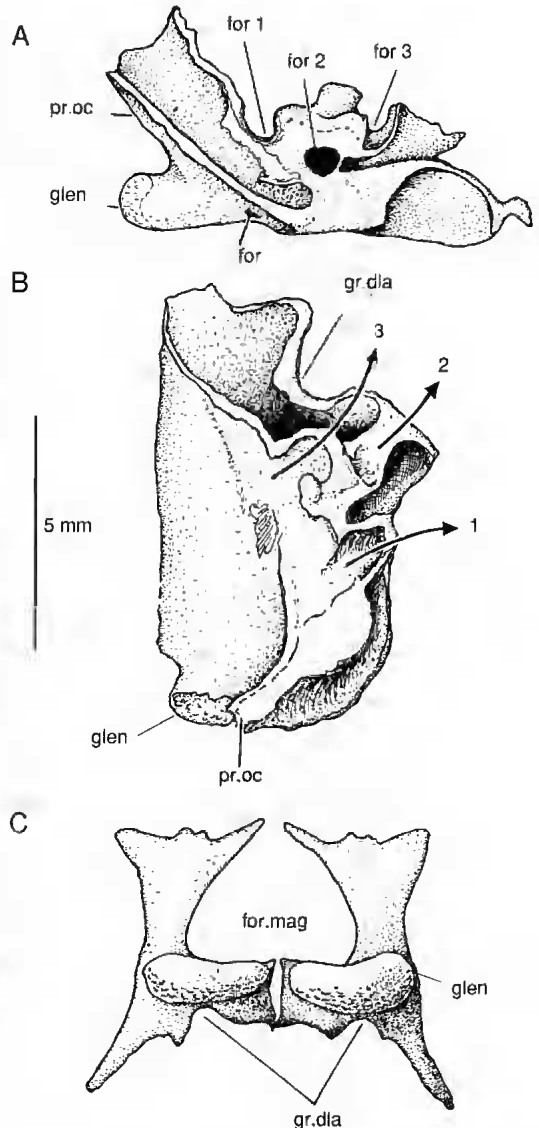


FIG. 32. — *Austroptyctodus gardineri* (Miles et Young, 1977) n.g. WAM 86.9.662. **A, B**, right occipital ossification of braincase; **A**, mesial view; **B**, lateral view, **C**, reconstruction of posterior view of braincase. **for.**, for 1, 2, 3, foramen or identified series of foramina; **for.mag**, foramen magnum of endocranium; **glen**, glenoid condyle of endocranium; **gr.dla**, groove for one branch of the dorsolateral aorta; **pr.oc**, ascending occipital process of braincase.

artery (also located in this position in *Brindabellaspis*, Young 1980, figs 7, 8).

#### Orbital ossification

The orbital ossification figured by Miles & Young (1977) was interpreted on the basis of its presumed orientation. They restored it as lying vertically behind the orbital cavity based on one specimen (P50908), with the structure interpreted as the attachment for an eyestalk located far posterior of the eyeball. The foramina for transmitting vessels or nerves were thus seen passing from within the braincase to the orbital cavity. Specimens of *Ctenurella gladbachensis* show that the orbital ossifications are always joined mesially and lie within the orbit, implying that they may have been positioned horizontally in life, thus forming the ventral wall of the orbital cavity. This interpretation is further supported by Eichwald's (1859) figured articulated specimen of *Chelyophorus verneuili*, which shows in ventral view the paired occipital ossifications *in situ* (Fig. 31), with one of the paired orbital ossifications lying just anterior to these. An excellent specimen of an orbital ossification of *Chelyophorus verneuili* in the MNHN collections has been freed from the matrix and is figured here alongside those of the *Austroptyctodus* specimens (Fig. 33C, D) to illustrate further the morphology of this bone. Additional evidence for the horizontal position of the orbital ossification is provided by the extensive mesial lamina of the marginal plate in both Gogo ptyctodontids, in which an extensive dorsal lamina is developed, and which still bears its connection to the orbital ossification in the holotype specimen of *Austroptyctodus gardineri*.

I have restored the orbital ossifications as being oriented transversely and longitudinally below the orbit, in mesial contact with each other, connected by cartilage to the dorsal, mesially directed shelf above the perichondral cone, for the posterior postorbital process of the endocranium (Fig. 34). This is based on several pieces of evidence:

1. Their position in the articulated specimen WAM 86.9.662 (orb.oss; Figs 28, 29) in which the paired orbital ossifications lay very close to each other, a short distance anterior to the paired occipital ossifications (seen in ventral view) and

in close proximity to the ethmoid ossification.

2. In the holotype of *Austroptyctodus gardineri* the orbital ossification is articulated with the mesial perichondral process of the marginal plate, suggesting horizontal alignment as the mesial lamina of the marginal is horizontal in life position.

3. The fact that they are joined mesially in some specimens of *Ctenurella gladbachensis*.

4. The fact that the articulated, uncrushed specimen of *Chelyophorus verneuili* shows the horizontal position of the orbital ossifications in continuity with the horizontal laminae of the occipital ossifications (see Fig. 31).

The orbital ossifications are seen to lie in the transverse plane forming the central division of the ventral endocranial wall, most of which forms the extensive subocular shelf. The dorsally elevated process on the lateral margin of the orbital ossification is most likely an eyestalk attachment, situated more to the anteromesial part of the orbit, as it is in other placoderms (e.g. *Buchanosteus*, *Brindabellaspis*, Young 1986).

A large robust articulation, lying to the anterolateral corner of the orbital ossification, can be interpreted as a strong cartilaginous connection to the perichondral, thickening on the visceral surface of the marginal plate, thus bracing the lateral wall of the endocranium with the marginal plate. In this respect it is most possibly an homologue of the posterior postorbital process of other placoderms, which abuts the marginal plate in arthrodirees (*Buchanosteus*, Young 1979). It appears to be too posteriorly situated either for the opercular cartilage or for hyomandibular articulation to the braincase, which are located adjacent to the ethmoid ossification and can be seen by the anterior position of the head of the submarginal plate with respect to the orbit on articulated specimens of both *Ctenurella gladbachensis* and *Austroptyctodus gardineri*.

The two foramina piercing the orbital ossification are small in comparison with those for the major nerves in placoderms, and do not pass from the brain cavity, but from the ventral surface of the endocranium into the orbital region. These foramina are clearly seen in the isolated orbital ossification of *Chelyophorus verneuili* (Fig. 33C, D) but they are so small in the Gogo specimen that they tend to be obscured by the

consolidating glue and are seen as depressions (Fig. 33). Thus, only one large canal is seen penetrating the bone near the eyestalk attachment in the Gogo specimen, and this is possibly the canal for the orbital artery (orb.a; Fig. 33). A larger canal more posteriorly situated on the orbital ossification of *Chelyophorus*, emerging from a well-defined pit on the dorsal surface (orbital cavity), is most likely for the internal carotid artery emerging from the ventral myo-

dome (i.car, v.my; Fig. 33C, D) which in *Dicksonosteus* (Goujet 1984a) and *Brindabellaspis* (Young 1980) runs up through the subocular shelf and into the ventral myodome for the eye muscles. Other smaller foramina which do not seem to penetrate through the ossification may be vascular supply canals for the interperichondrium.

There are two well defined notches embayed into the lateral margins of the orbital ossifications in

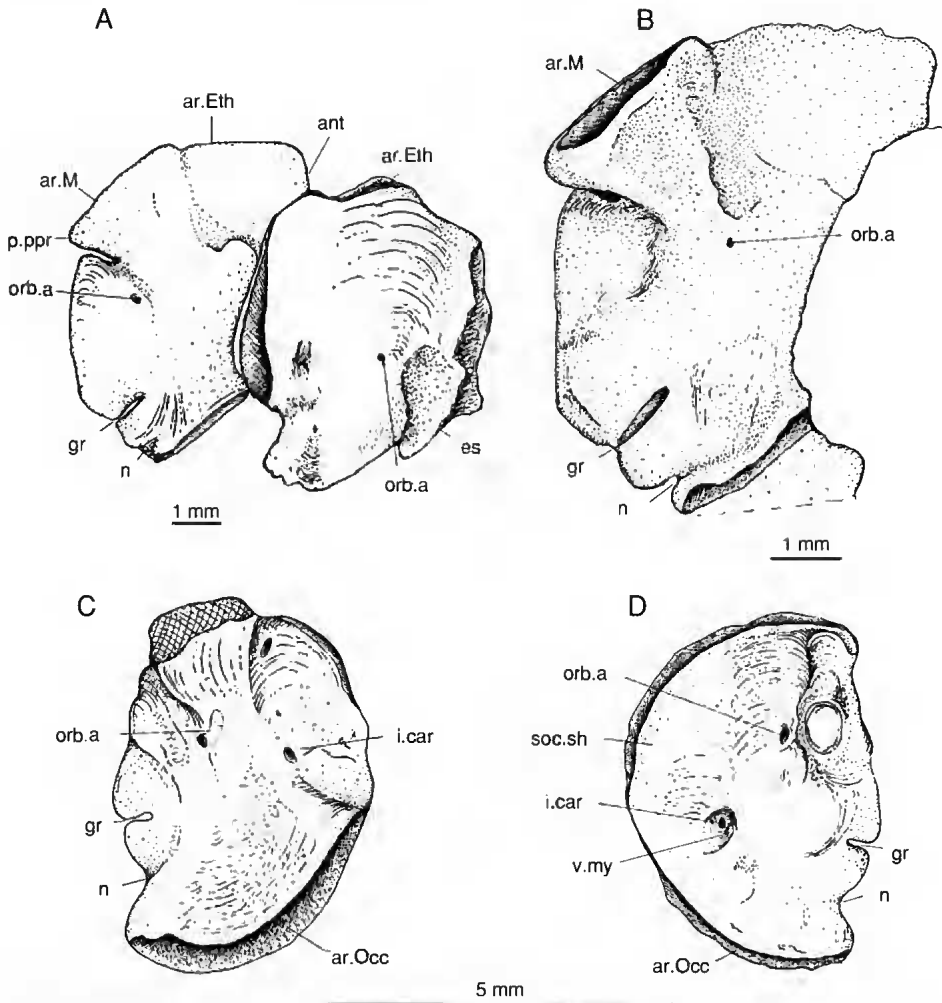


FIG. 33. — *Austroptyctodus gardineri* n.g. (Miles et Young, 1977). WAM 86.9.662, orbital ossifications of braincase. **A**, paired units as preserved (see figures 27, 28 for position with respect to rest of specimen); **B**, detail of left orbital ossification in ventral view. **C**, **D**, *Chelyophorus verneuili* Agassiz, 1844, MNHN specimen, Agassiz type collection (unnumbered, Collection of Verneuil, Laboratoire de Paléontologie, MNHN): left orbital ossification, **C**, ventral view; **D**, dorsal view. **ant.**, anterior direction; **ar.Eth**, articulation for ethmoid ossification; **ar.M**, articulation for marginal plate; **ar.Occ**, articulation for occipital ossification; **es**, eyestalk attachment; **gr**, groove; **i.car**, internal carotid foramen; **n**, notch; **orb.a**, foramen for orbital artery; **p.ppr**, possible homologue of the posterior postorbital process of endocranium; **soc.sh**, subocular shelf; **v.my**, ventral myodome.



both *Gogoptycodus* and *Chelyophorus* (gr, n; Fig. 33). As these are considerably larger than the arterial foramina, the largest of these, situated posterior to the eyestalk and internal carotid foramen, is possibly for the pituitary vein.

#### *Ethmoid ossification*

The ethmoid ossification has been well-described by Miles & Young (1977), but was not restored in relation to the rest of the endocranium and jaw suspensory mechanism. The new material adds nothing new to the description of the ethmoid ossification, as no isolated ethmoid ossifications have yet been recovered from the Russian material or the new Gneudna specimens. It should be noted that Ørvig (1962) restored the ethmoid ossification in *C. gladbachensis* with a large anteriorly facing articulatory facet for the palatoquadrate, and labelled it as the "metapterygoid". It seems likely that the large anterior facets on the ethmoid faced anterolaterally, as suggested by Miles & Young, to articulate with the articulatory facets on the autopalatine, the midlines of the ethmoid ossifications meeting medially held by cartilage.

#### *Nasal ossification*

Observation of the Bergisch-Gladbach material of *Ctenurella gladbachensis* and of *Austroptyctodus gardineri* shows that the ethmoid ossification is always preserved in a position ventral to the "metapterygoids" of the palatoquadrate. In the holotype of *Austroptyctodus* (Miles & Young 1977; Fig. 23) the right "metapterygoid" is separated from the autopalatine and rests immediately dorsal to the ethmoid ossification, which clearly separates this ossification from the upper jaw ossifications. This leads me to propose that the "metapterygoid" has been misinterpreted and is actually not part of the upper jaw apparatus but could represent a paired nasal ossification partly enclosing the nasal capsules. These bones sit anterior to the orbits directly dorsal to the upper jaw ossifications (nas.oss; Fig. 35), in a position appropriate for the external nares by comparison with other placoderms. The shape of the ossification as described for *Austroptyctodus* by Miles & Young (1977, fig. 26) shows that the lateral face is concave and would have been able to support the

olfactory bulb, in a way similar to the preorbital recess of antiarchs, immediately anterior to the orbit. The presence of paired nasal ossifications is known in arthrodires as cribrosal bones, clearly seen in many of the Gogo eubranchyothoracids (e.g. *Eastmanosteus*, Dennis-Bryan 1987; *Latocamurus*, Long 1988c; plourdosteids, see Gardiner & Miles 1990). There is a groove and a ridge developed on the mesial side of the bone, noted by Miles & Young (1977: 176) as possibly being for attachment to the endocranium. The well-defined groove which runs dorsally and anteriorly above the cavity for the nasal capsule is possibly for a terminalis nerve, which has been identified mesial to the nasal capsules in the arthrodire *Latocamurus* (Long 1988c). The nasal ossifications had well-developed posterodorsal processes (Miles & Young 1977, "prmp1" fig. 26) which may have mesially been joined by ligaments. The function of this unusual process on the nasal ossifications could have been as an attachment region for the median rostral cartilage (m.ros.cart; Fig. 28), an ossification present in some ptyctodontids but absent in all other placoderms.

#### *Reconstruction of the endocranium*

A reconstruction of the endocranium in ptyctodontids was given by Miles & Young (1977, fig. 22) based on the available specimens of *Austroptyctodus gardineri*. In light of the new material and the evidence from new observations on the articulated position of braincase ossifications in both *Chelyophorus* and *Ctenurella*, it is now possible to provide a new sketch reconstruction of the ptyctodontid endocranium (Fig. 34). The position of the occipital ossifications is clear as the glenoid processes are always aligned with horizontal long axes, as correctly restored by Miles & Young (1977, fig. 22B, and shown here Fig. 32C), as it also occurs in the articulated specimen of *Chelyophorus* (Fig. 31). That the paired orbital ossifications lie in the horizontal plane below the orbit has been argued above from evidence seen in uncrushed articulated specimen of *Chelyophorus*, plus observations on the Gogo and Bergisch-Gladbach specimens. The relative sizes of the occipital, orbital, ethmoid and nasal ossifications in relation to the skull roof are clearly seen from WAM 96.9.662, upon which the dor-

sal view outline reconstruction of the endocranium was largely based. The position of the ethmoid ossifications immediately anterior to the orbital ossifications and articulating with the palatoquadrate is also based on observations of *Ctenurella* and of the WAM 86.9.662 specimen of *Austroptyctodus*. Finally, the position of the paired nasal ossifications, anterior to the ethmoid ossifications and sitting above the palatoquadrate and behind the inferred position of the nares, is a new interpretation based on observations of several specimens of articulated *Ctenurella* and *Austroptyctodus*.

The braincase of ptyctodontoforms, as restored herein, is unique amongst placoderms in comprising at least four paired perichondral components, forming a solid floor to the endocranium but lacking any dorsal ossification. Furthermore it is unlike any other placoderm in having a median suture running down its midline where opposite sides of the paired ossifications are joined by cartilage. The rounded shape of the orbital ossifications implies that a space exists anterior to the mesial connection between these units and the ethmoid ossifications immediately anterior to them. This could be for a ventral hypophysial

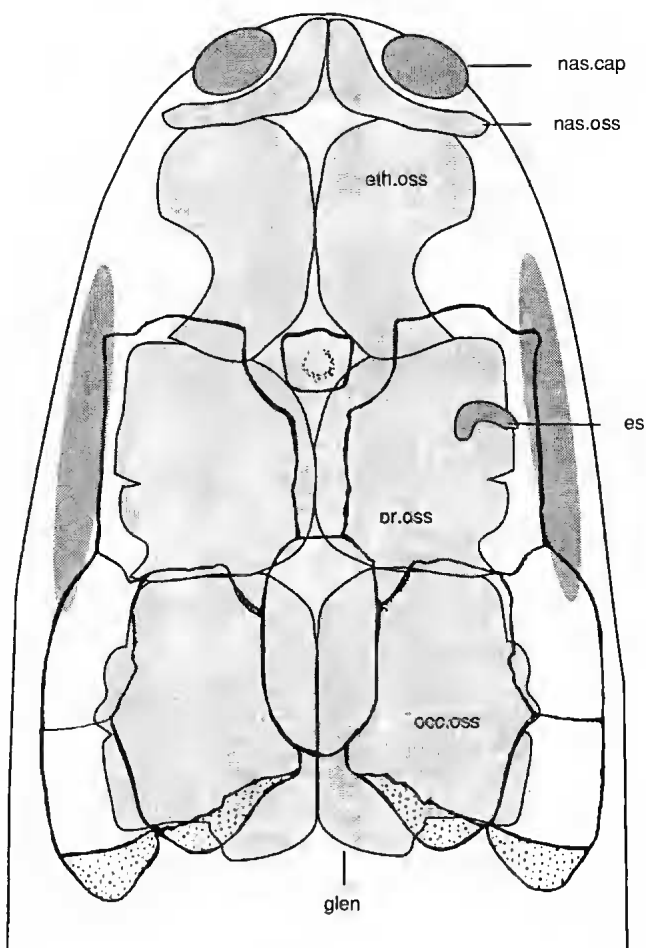


FIG. 34. — Attempted reconstruction of the endocranium in dorsal view (shaded) of *Austroptyctodus gardineri* (Miles et Young, 1977) n.g., based largely on WAM 86.9.662. Outline of skull roof bones shown as transparent. *es*, eyestalk attachment; *eth.oss*, ethmoid ossification of endocranium; *glen*, glenoid condyle of endocranium; *nas.cap*, nasal capsule; *nas.oss*, nasal ossification of endocranium; *occ.oss*, occipital ossification of endocranium; *or.oss*, orbital ossification of endocranium.

opening. There is no parasphenoid ossification as in arthrodires, phyllolepid and in the acanthothoracid *Kosoraspis*.

Figure 35 provides a revised reconstruction for the dermal exoskeleton and visceral skeleton, as known for *Austroptyctodus gardineri*.

#### Dermal scales

Thin scales covered the tail of *Austroptyctodus gardineri*, as preserved in WAM 86.9.662 (sc; Figs 27-29). They closely resemble those of *Campbellodus* in overall form, being boomerang-shaped, much higher than long in the articulated squamation, with a dorsal external lamina and a

ventral overlapped region. The external ornamentation is a very fine reticulate pattern.

#### SUMMARY AND CONCLUSIONS

1. The genus *Campbellodus decipens* Miles et Young is redescribed from a complete new specimen, showing it to have three median dorsal plates, a dermal scale cover and well-ossified anterior gill arch series. The skull roof shows that the preorbitals plates did not suture in the midline, as it is now known to occur in some other

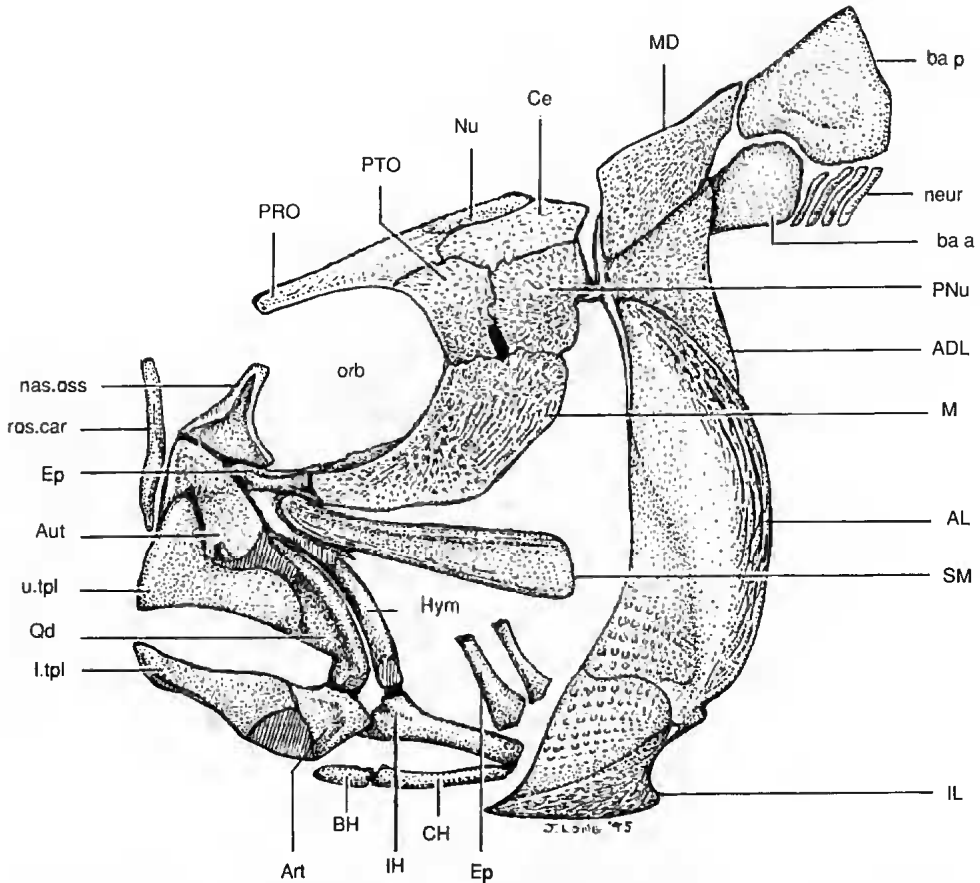


FIG. 35. — Attempted reconstruction of the dermal exoskeleton and visceral endoskeleton of *Austroptyctodus gardineri* n.g. (Miles et Young, 1977), based largely on WAM 86.9.662 and on the holotype, WAM 70.4.253. ADL, anterior dorsolateral plate; AL, anterior lateral plate; Art, articular; Aut, Autopalatine; ba a, ba p, anterior and posterior basal plates; BH, basihyal; Ce, central plate; CH, ceratohyal; Ep, epibranchials; Hym, hyomandibular; IH, interhyal element; IL, interolateral plate; l.tpl, lower tooth plate; M, marginal plate; MD, MD1, 2, 3, median dorsal plate(s) or spines; nas.oss, nasal ossification of endocranium; neur, neural arches; Nu, nuchal plate (posterior element); orb, orbit; PNu, paranuchal plate; PRO, preorbital plate; PTO, postorbital plate; Qd, quadrate; ros.car, rostral cartilages (paired); SM, submarginal plate; u.tpl, upper tooth plate.

ptyctodontids (e.g. *Austroptyctodus* n.g., *Rhynchodus tetradon*).

2. The large, posteroventrally directed gill arch bones that lie immediately behind the jaw articulation in ptyctodontids had previously been interpreted as "ceratohyals" in *Ctenurella* and in the Gogo form *Austroptyctodus*. New evidence from *Campbellodus* and *Austroptyctodus* n.g. suggests that these are modified interhyal elements and that the ceratohyals are large, deep bones, as occur in *Campbellodus*.

3. Revision of some Bergisch-Gladbach specimens of *Ctenurella gladbachensis* Ørvig, 1960 shows that the skull roof had been incorrectly restored, and that the centrals do in fact meet each other behind the nuchal plate. A revised diagnosis of the genus is given.

4. "*Ctenurella*" *gardineri* Miles et Young, 1977 is shown to differ from *Ctenurella gladbachensis* in the arrangement of skull roof bones and body squamation, and is here referred to a new genus, *Austroptyctodus gardineri* n.g.

5. The braincase in ptyctodontids is interpreted to comprise at least four paired perichondral ossifications, the occipital, orbital, ethmoid and nasal units. The latter was previously identified as being the "metapterygoid". Perichondral units attached to the inside of the marginal plate may have housed the posterior postorbital process of the endocranium, as in other placoderms. Ptyctodontids apparently lacked a parasphenoid.

### Acknowledgments

The new specimens of Gogo ptyctodontids were collected in 1986 by the author whilst under the support of the National Geographic Society of America (grant #3364-86). I also thank Prof. P. Taquet and Dr. P. Janvier for offering me a visiting professor position for three months and providing research facilities (September–November 1995), and the Trustees of the Western Australian Museum for supporting this research proposal. My colleagues in France gave freely of their time and discussed various aspects of the work, I am especially grateful to Drs P. Janvier, D. Goujet, H. Lelièvre and Z. Min. Thanks also to Dr P. Forey of the Natural History Museum, London, who gave access to the collections and discussed aspects of

the work. I thank Dr. L. Grande for access to collections in the Field Museum, Chicago, in April 1996, and to B. Hickerson, Augustana College, Illinois, for showing me his new finds of ptyctodontids from the Spring Grove Member. Drs D. Goujet and G. Young are thanked for discussing aspects of the work and reviewing the manuscript. For some of the photographs of Gogo specimens, I thank Ms K. Brimmell, and for some of the Gogo specimen drawings, I thank Miss D. Hendricks.

### REFERENCES

- Agassiz L. 1844. — *Monographie des poissons fossiles du vieux grès rouge ou système Dévonien (Old red sandstone) des îles britanniques et de Russie*. Neuchâtel, 171 p.
- Blicek A., Golshani F., Goujet D., Hamdi A., Janvier P., Mark-Kurik E. & Martin M. 1980. — A new vertebrate locality in the Eifelian of the Khush-Yeilagh Formation, Eastern Alborz, Iran. *Palaeovertebrata*, Montpellier 9: 133-154.
- Brunton C. H. C., Miles R. S. & Rolfe W. D. I. 1969. — Gogo expedition 1967. *Proceedings of the Geological Society of London* 1655: 80-83.
- Campbell K. S. W. & Barwick R. E. 1988. — *Uranolophus*; a reappraisal of a primitive dipnoan. *Memoirs of the Association of Australasian Palaeontologists* 7: 87-144.
- Carl R. K. 1991. — Reanalysis of *Heintzichthys gouldii* (Newberry), an aspinothoracid arthrodire (Placodermi) from the Famennian of northern Ohio, with a review of brachythoracid systematics. *Zoological Journal of the Linnean Society* 103: 349-390.
- 1995. — Placoderm diversity and evolution. *Bulletin du Muséum national d'Histoire naturelle*, Paris, série 4, C 17 (1-4): 85-125.
- Denison R. H. 1978. — Placodermi, in H-P. Schultze (ed.), *Handbook of Paleozoichthyology*. Pt 2. Gustav Fischer Verlag, Stuttgart, New York, 128 p.
- 1984. — Further consideration of the phylogeny and classification of the Order Arthrodira (Pisces: Placodermi). *Journal of Vertebrate Paleontology* 4: 396-412.
- 1985. — A new ptyctodontid placoderm, *Ptyctodopsis*, from the Middle Devonian of Iowa. *Journal of Paleontology* 59: 511-522.
- Dennis-Bryan K. 1987. — A new species of eastmanosteid arthrodire (Pisces: Placodermi) from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 90: 1-64.
- Dollo L. 1907. — Les ptyctodontes sont des arthrodires. *Bulletin de la Société belge, Géologie et*

- Paléontologie, Hydrologie* 9 : 79-128.
- Eichwald E. 1859. — *Lethaea Rossica ou paléontologie de la Russie*. Premier volume : ancienne période. Stuttgart, 1657 p.
- Forey P. L. & Gardiner B. G. 1986. — Observations on *Ctenurella* (Ptyctodontida) and the classification of placoderm fishes. *Zoological Journal of the Linnean Society* 86: 43-74.
- Gardiner B. G. 1984a. — The relationships of placoderms. *Journal of Vertebrate Paleontology* 4: 379-395.
- 1984b. — Relationships of the palaconiscoid fishes, a review based on new specimens of *Mimia* and *Moythamasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum of Natural History (Geology)* 37: 173-428.
- Gardiner B. G. & Miles R. S. 1975. — Devonian fishes of the Gogo Formation, Western Australia. *Colloque International du CNRS* 218 : 73-79.
- 1990. — A new genus of eubranchyothoracid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 99: 159-204.
- Goodrich E. S. 1909. — "Vertebrata craniata 1: Cyclostomes and Fishes", in Lankester R., *Treatise on Zoology* 9, 518 p.
- Goujet D. 1984a. — Placoderm interrelationships: a new interpretation, with a short review of placoderm classifications. *Proceedings of the Linnean Society of New South Wales* 107: 211-243.
- 1984b. — Les poissons placodermes du Spitzberg. Arthrodirés Dolichothoraci de la Formation de Wood Bay (Dévonien inférieur). *Cahiers de Paléontologie*, éd. CNRS, Paris, 284 p.
- Goujet D. & Young G. C. 1995. — Interrelationships of placoderms revisited. *Geobios*, M.S. 19 : 89-96.
- Gross W. 1933. — Die unterdevonischen Fischen und Gigantostraken von Overath. *Abhandlungen Preuss Geologische Landesanstalt N.F.*, 145: 41-77.
- 1961. — *Lunaspis broilli* und *L. heraldi* aus dem Hunsruckscheifer (Unterdevon; Rheinland). *Hessisches Landesamt für Bodenforschung, Notizblatt*, Weisbaden 89: 17-43.
- 1963. — *Gemuendina stuerzi* Traquair. Neuuntersuchung. *Hessisches Landesamt für Bodenforschung, Notizblatt*, Wiesbaden 91: 36-73.
- Hickerson W. 1993. — Ptyctodontid placoderms? from the Upper Spring Grove Member of the Pinicon Range Formation. *Geological Society of Iowa Guidebook* 59: 45-54.
- Jaekel O. 1903. — Über *Rhamphodus* n. gen., einen neuen devonischen Holocephalen von Wildungen. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*.
- 1906. — Einige Beiträge zur morphologie der ältesten Wirbelthiere, *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 180.
- Jarvik E. 1972. — Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n.sp. *Meddelelser om Grønland* 187 (2): 1-295.
- 1980. — *Basic Structure and Evolution of Vertebrates*. Vol. 2. Academic Press, London, New York.
- Johnson H.-M. & Elliott D. (in press). — A new ptyctodont (Placodermi) from the Upper Devonian Martin Formation of Northern Arizona, and an analysis of Ptyctodont phylogeny. *Journal of Vertebrate Paleontology*.
- Lebedev O. 1995. — Morphology of a new osteolepidid fish from Russia, in Arsenault M., Lelièvre H. & Janvier P. (eds), Studies on Early Vertebrate (VII<sup>e</sup> International Symposium, 1991, Miguasha Parc, Québec). *Bulletin du Muséum national d'Histoire naturelle*, Paris, série 4, C 17 (1-4) : 287-342.
- Lelièvre H. 1995. — Description of *Maideria falipoui* n.g., n.sp., a long snouted brachyothoracid (Vertebrata, Placodermi, Arthrodira) from the Givetian of Maider (South Morocco), with a phylogenetic analysis of primitive brachyothoracids, in Arsenault M., Lelièvre H. & Janvier P. (eds), Studies on Early Vertebrate (VII<sup>e</sup> International Symposium, 1991, Miguasha Parc, Québec). *Bulletin du Muséum national d'Histoire naturelle*, Paris, série 4, C 17 (1-4) : 163-207.
- Lelièvre H., Janvier P. & Goujet D. 1981. — Les Verrébrés Dévoniens de l'Iran central. IV. Arthrodirés et ptyctodontes. *Geobios* 14 : 677-709.
- Liem K. F. 1993. — Ecomorphology of the teleostean skull. Ch. 10: 422-452, in Hanken J. & Hall B. K. (eds), *The Skull. 3. Functional and Evolutionary Mechanisms*. University of Chicago Press.
- Liu Y.-H. 1991. — On a new petalichthyid, *Eurycaraspis incilis* gen. et sp. nov. (Placodermi, Pisces) from the Middle Devonian of Zhanyi; Yunnan: 139-177, in Chang M. M., Liu Y. H. and Zhang G. R. (eds), *Early Vertebrates and related problems of evolutionary biology*. Science Press, Beijing.
- Long J. A. 1984a. — A plethora of placoderms: the first vertebrates with jaws? 185-210, in Archer M. & Clayton G. (eds), *Vertebrate Zoogeography and Evolution in Australasia*. Hesperian Press, Carlisle, Western Australia.
- 1984b. — New phyllolepid from Victoria and the relationships of the group. *Proceedings of the Linnean Society of New South Wales* 107: 263-304.
- 1987. — Late Devonian fishes from the Gogo Formation, Western Australia. New discoveries. *Search* 18 (4): 203-205.
- 1988a. — Late Devonian fishes from Gogo, Western Australia. *National Geographic Research* 4: 436-450.
- 1988b. — ? *Campbellodus* sp. (Placodermi: Ptyctodontida) from the Upper Devonian Napier Range, Canning Basin. *Records of the Western Australian Museum* 14: 141-144.
- 1988c. — A new camuropiscid arthrodira (Pisces: Placodermi) from Gogo, Western Australia.

- Zoological Journal of the Linnean Society* 94: 233-258.
- 1990b. — Two new arthrodires (placoderm fishes) from the Upper Devonian Gogo Formation, Western Australia. *Memoirs of the Queensland Museum* 28: 51-63.
  - 1991. — The long history of Australian fossil fishes. Ch.12: 337-428, in Rich P. V., Monaghan J., Baird R. F. & Rich T. (eds.), *The Vertebrate Palaeontology of Australasia*, Pioneer Design Studios, Lilydale.
  - 1994a. — A second incisoscutid arthrodire from Gogo, Western Australia. *Alcheringa* 18: 59-69.
  - 1994b. — A new groenlandaspidid arthrodire (Pisces; Placodermi) from the Middle Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Records of the Western Australian Museum* 17: 35-41.
  - 1995a. — A new plourdosteid arthrodire from the Late Devonian Gogo Formation, Western Australia: systematics and phylogenetic implications. *Palaeontology* 38: 39-65.
  - 1995b. — *The Rise of Fishes-500 Million Years of Evolution*. Johns Hopkins University Press, Baltimore; University of New South Wales, Press, Sydney, 230 p.
- Mark-Kurik E. 1977. — The structure of the shoulder girdle in early ptyctodontids, in Menner V. V. (ed), *Ocherki po filogenii i sistematike iskopaemykh ryb i beschechuystnykh*: 61-70 [in Russian].
- Miles R. S. 1967. — Observations on the ptyctodontid fish *Rhamphodopsis* Watson. *Zoological Journal of the Linnean Society* 47: 99-120.
- 1971. — Palaeozoic fish. *McGraw Hill Yearbook of Science and Technology* 1971: 312-314.
  - 1973. — Relationships of acanthodians, in Greenwood P. H., Patterson C. & Miles R. S. (eds), *Interrelationships of Fishes*: 63-103.
  - 1977. — Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zoological Journal of the Linnean Society* 61: 1-328.
- Miles R. S. & Westoll T. S. 1968. — The placoderm fish *Cocosteus cuspidatus* Miller ex Agassiz from the Middle Old Red Sandstone of Scotland. Part 1. Descriptive morphology. *Transactions of the Royal Society of Edinburgh* 67: 373-476.
- Miles R. S. & Young G. C. 1977. — Placoderm interrelationships reconsidered in the light of new ptyctodontids from Gogo Western Australia. *Linnean Society of London, Symposium Series* 4: 123-198.
- Newberry J. S. 1873. — Descriptions of fossil fishes. Ohio. *Geological Survey Report* 1, pt. 2 (Paleontology): 245-355.
- Obrucheva D. 1983. — On *Chelyaphorus* from the Central Devonian field: 28-35 [in Russian], in *Current Problems in Palaeoichthyology*. Moscow Society of Naturalists, Palaeontological Institut, Nauka, Moscow.
- Ørvig T. 1960. — New finds of acanthodians, arthrodires, crossopterygians, ganoids and dipnoans in the Upper Middle Devonian-Calcareous Flags (Oberer Plattenkalk) of the Betgisch-Paffrath Trough. (Part 1). *Paläontologische Zeitschriften* 34: 295-335.
- 1962. — Y a-t-il une relation directe entre les arthrodires ptyctodontides et les holocéphales? *Colloque International du CNRS* 104: 49-61.
  - 1971. — Comments on the lateral line system of some brachyothoracid and ptyctodontid arthrodires. *Zoologica Scripta* 1: 5-35.
  - 1975. — Description, with special reference to the dermal skeleton, of a new radonid arthrodire from the Gedinian of Arctic Canada. *Colloque International du CNRS* 218: 41-71.
  - 1980. — Histologic studies of ostracoderms, placoderms and fossil elasmobranchs. Ptyctodontid tooth plates and their bearing on holocephalan ancestry: the condition in chimaerids. *Zoologica Scripta* 14: 55-79.
- Pander C. H. 1858. — *Über die Ctenodipterinen des devonischen Systems*. Saint Petersburg, 53 p.
- Patterson C. 1965. — The phylogeny of the chimaeroids. *Philosophical Transactions of the Royal Society of London* 249 B: 101-219.
- Ritchie A. 1973. — *Wuttagoonaspis* n.g., an unusual arthrodire from the Devonian of western New South Wales. *Palaeontographica* 143 A: 58-72.
- 1984. — A new placoderm, *Placolepis* n.g. (Phyllolepididae) from the Late Devonian of New South Wales. *Proceedings of the Linnean Society of New South Wales* 107: 321-354.
- Schultze H.-P. 1993. — Patterns of diversity in the skulls of jawed fishes. Ch. 5: 189-254, in Hanken J. & Hall B. K. (eds), *The Skull. Vol. 2. Patterns of Structural and Systematic Diversity*. University of Chicago Press.
- Smith B. G. 1937. — The anatomy of the frilled shark *Chlamydoselachus anguineus* Garman. *Bashford Dean Memorial Volume Vol. II*, The American Museum of Natural History, New York: 331-520.
- Stahl B. J. 1967. — Morphology and relationships of the Holocephali with special reference to the venous system. *Bulletin of the Museum of Comparative Anatomy Harvard* 135: 141-213.
- Stensjö I. A. 1959. — On the pectoral fin and shoulder girdle of the arthrodires. *Kungliga Svenska Vetenskap Akademiens Handlingar* 8: 1-229.
- 1963. — Anatomical studies on the arthrodiran head. Part 1. Preface, geological and geographical distribution, the organisation of the arthrodires, the anatomy of the head in the Dolichothoraci, Cocosteomorphi and Pachyosteomorphi. Taxonomic appendix. *Kungliga Svenska Vetenskap Akademiens Handlingar* 4 (9) 2: 1-419.
  - 1969. — Elasmobranchiomorphi Placodermata Arthrodires: 71-692, in Piveteau J. P. (ed), *Traité*



- de Paléontologie*. Masson, Paris.
- Veran M. 1988. — Les éléments accessoires de l'arc hyoïdien des poissons téléostomes (Acanthodiens et Osteichthyens fossiles et actuels). *Mémoires du Muséum national d'Histoire naturelle*, série C 54 : 13-98.
- Watson D. M. S. 1934. — The interpretation of arthrodires. *Proceedings of the Zoological Society of London* 3: 437-464.
- 1938. — On *Rhamphodopsis*, a ptyctodont from the Middle Old Red sandstone of Scotland. *Transactions of the Royal Society of Edinburgh* 59: 397-410.
- Woodward A. S. 1891. — *Catalogue of the fossil fishes in the British Museum (Natural History)*. Volume 2. British Museum, Taylor & Francis, London, 567 p.
- 1941. — The head shield of a new macropetalichthyid (*Notopetalichthys hillsi* gen. et sp. nov.) from the Middle Devonian of Australia. *Annals and Magazine of Natural History* 8: 91-96.
- Young G. C. 1979. — New information on the structure and relationships of *Buchanosteus* (Placodermi: Euarthrodira) from the Early Devonian of New South Wales. *Zoological Journal of the Linnean Society* 66: 309-352.
- 1980. — A new Early Devonian placoderm from New South Wales, Australia, with a discussion of placoderm phylogeny. *Palaeontographica* 167A: 10-76.
- 1981. — Biogeography of Devonian vertebrates. *Alcheringa* 5: 225-243.
- 1984. — Reconstruction of the jaws and braincase in the Devonian placoderm fish *Bothriolepis*. *Palaeontology* 27: 625-661.
- 1985. — New discoveries of Devonian vertebrates from the Amadeus Basin, central Australia. *BMR Journal of Australian Geology and Geophysics* 9: 239-254.
- 1986. — The relationships of placoderm fishes. *Zoological Journal of the Linnean Society* 88: 1-57.
- Young G. C., Long J. A. & Turner S. 1993. — Appendix 1. Faunal lists of eastern Gondwana Devonian macrovertebrate assemblages: 246-251, in Long J. A. (ed.), *Paleozoic Vertebrate Biostratigraphy and Biogeography*. Belhaven Press, London.
- Young G. C. & Zhang G.-R. 1992. — Structure and function of the pectoral joint and operculum in antiarchs, Devonian placoderm fishes. *Palaeontology* 35: 443-464.

*Submitted for publication on 14 June 1996;  
accepted on 5 November 1996.*